Succession and disturbance in a successional gradient: impact of crucial abiotic and biotic factors

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„Und wenn Natur dich unterweist,
Dann geht die Seelenkraft dir auf.“
Faust. Der Tragödie Erster Teil, J.W. von Goethe

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1. Chapter 1

General introduction

Open ecosystems in Central Europe are threatened mainly due to changes in agricultural land use (Ssymank et al. 1998). Reasons include, for example, the abandonment of extensively used grassland, eutrophication or fragmentation. Consequences of fragmentation are the reduction of habitat size and, hence, the spatial isolation of populations (Saunders et al. 1991). The risk of local extinctions increases with declining population size (Fischer & Stöcklin 1997). Therefore the reproduction success of many rare plant species in various habitats is reduced (Neugebauer 2001; Brys et al. 2004; Kéry & Matthies 2004). Target species need support by nature conservation measures in order to (re-)colonise suitable habitats successfully.

Various management methods for low-productive ecosystems have been discussed, for instance mowing, mulching, burning or grazing (Moog et al. 2002). Especially sheep grazing has turned out to be an adequate conservation tool in inland sand ecosystems (Stroh et al. 2002; Hellström et al. 2003; Schwabe et al. 2004; Schwabe & Kratochwil 2004). Herbivores affect colonisation patterns of species by grazing, trampling and deposition of faeces (Harper 1977; Bakker & Olff 2003). In grasslands disturbance and gap creation play an important role for the regeneration of species and the maintenance of species diversity (Bakker & Olff 2003). This applies particularly to inland sand ecosystems (Jentsch et al. 2002; Jentsch 2004; Schwabe & Kratochwil 2004). Here, the impact of sheep grazing countered spontaneous succession and furthermore it was beneficial for the plant species richness (Süss et al. 2004). If disturbance dynamics in grasslands cease, competitive graminoids become dominant and inhibit the regeneration of target species (Kooijman & van der Meulen 1996; Süss et al. 2004; Bakker 2005). In this case non-typical succession lines and further ruderalisation processes cannot be excluded.

Recently, a decrease of diversity together with ruderalisation was reported for many ecosystems (Welch & Scott 1995; Hölzel & Otte 2003; Bischoff 2005). Increasing nitrogen-immissions can be a reason for the increase of ubiquitous plants, which are often nitrophytes (ten Harkel & van der Meulen 1995; Kooijman & van der Meulen 1996). Especially early successional grassland stages with poorly competitive species are endangered habitats in Central Europe (Schwabe et al. 2002) and were so classified according to the European conservation program Natura 2000 (Ssymank et al. 1998). These pioneer sandy grasslands are inhabited by a high diversity of site-specific plant species, which are adapted to dry and nutrient-poor conditions. Consequently, their habitats are sensitive to changes in land-use and nitrogen immissions.

Plants have developed two main dispersal patterns: dispersal in time, mainly due to the formation of seed banks, and dispersal in space, due to transportation via vectors. Both strategies are major aspects of plant population dynamics (Harper 1977). The transport of diaspores by large herbivores as biotic vectors is significant for plant populations in fragmented landscapes in Europe and was recently emphasised by several authors (e.g., Poschlod et al. 1998; Bruun & Fritzbøger 2002; Couvreur et al. 2004, 2005; Cosyns & Hoffmann 2005; Eichberg et al. 2007; Wessels et al. 2008). In general, dispersal by grazing animals can take place via internal (endozoochory) or external transport (epizoochory). The post-dispersal fate of epizoochorously dispersed seeds was first studied by Eichberg et al. (2005), who showed the importance of trampling by incorporation of seeds in the soil substrate. Concerning the fate of dung-embedded seeds after endozoochorous dispersal, the emergence success depends mainly on microsite availabilities, which was studied for instance by Malo & Suárez (1995), Mouissie et al. (2005) or Cosyns et al. (2006), whereas Eichberg et al. (2007) demonstrated that the emergence success in the field was highest among target species.

Succession

Succession is subject to general principles like the replacement of species (Egler 1954) or facilitation processes (Connell & Slatyer 1977; Leuschner & Rode 1999). It is influenced by abiotic and biotic factors. For example, soil nitrogen as one abiotic factor can influence all successional stages (Tilman 1987; Olff et al. 1993; Chapin III et al. 2002). As an example for biotic factors, competitive plant species with high cover values are able to prevent the establishment of other vascular plant species due to the production of large amounts of litter which reduce germination opportunities, and this can lead to a retardation of further successional processes (Tilman 1987).

Typically, the successional pathway in base-rich inland sand ecosystems leads from pioneer stages of the classes Koelerio-Corynephoretea to species-rich stands of Allio-Stipetum vegetation (Süss et al. 2010). Often a ruderalisation tendency during succession of inland sand ecosystems can be observed (Stroh et al. 2002). Furthermore, a development into ruderalised species-poor stands was described in habitats with nutrient enrichment, which are dominated by tall competitive graminoids (Süss et al. 2004). Disturbance dynamics are crucial for threatened sand vegetation (Eichberg et al. 2007). Hence, extensive livestock grazing is important to ensure these dynamics, and it became a necessary tool to counteract ruderalised successional pathways and maintain species diversity (Schwabe & Kratochwil 2004; Schwabe et al. 2004; Süss et al. 2004; Eichberg et al. 2007).

Nutrients

Beside disturbance dynamics, nutrient limitation and status are crucial in many terrestrial ecosystems and can determine diversity in natural and semi-natural grasslands in Europe (Ellenberg & Leuschner 2010). In general, nutrient availability plays an important role for the species composition (Fridley 2002; de Deyn et al. 2004), but especially pioneer sand ecosystems are dependent on low nutrient levels and this is a decisive factor for the site-specific and threatened plant species among this community. Many studies have dealt with nitrogen as the main factor limiting plant productivity (Atkinson 1973; Bobbink 1991; Olff et al. 1993; Gough et al. 2000; Mamolos et al. 2005), but also phosphorus can play a crucial role, especially in sandy grasslands (Morecroft et al. 1994; Kooijman et al. 1998; Wassen et al. 2005; Hejcman et al. 2007; Storm & Süss 2008). Additionally, enhanced airborne nitrogen depositions are considered to cause grass encroachment, the increase of ruderals and the decrease of site-specific or endangered species (Bobbink et al. 1998; Gough et al. 2000).

Open habitats like pioneer sandy grasslands are very sensitive to nutrient enrichment, which may come along with a ruderalisation during succession and the development into species-poor mid-successional grasslands with a few monodominant species (Kooijman & van der Meulen 1996; Stroh et al. 2002; Poschlod et al. 2009; Süss et al. 2010). Early successional sand ecosystems are typically low-productive habitats and the typical community composition is depended on a low nutrient status (Storm & Süss 2008).

Grazing

Besides mowing, burning or mulching, predominantly extensive livestock grazing regimes have become important management tools regarding nature-conservation objectives in low-productive grasslands (Kooijman & van der Meulen 1996; Provoost et al. 2002; Hellström et al. 2003). Ungrazed grasslands are often dominated by tall grasses or perennial species (Noy-Meir et al. 1989). In threatened sand ecosystems grazing by sheep is an appropriate way to ensure vegetation dynamics due to intermediate disturbances and prevent grass encroachment or counteract ruderalisation (Stroh et al. 2002; Schwabe & Kratochwil 2004; Schwabe et al. 2004). The creation of microsites by, e.g., trampling, scratching and rolling (Zobel et al. 2000), and the dispersal of seeds via epi- or endozoochorous processes were considered beneficial for a successful establishment of plants in sandy grasslands (Eichberg et al. 2007; Süss & Schwabe 2007). Furthermore, selective grazing and phytomass extraction, respectively, and an influence on nutrient fluxes are important effects of herbivores (Bakker et al. 2004). Nevertheless, negative disturbance effects like overgrazing can be caused for instance by large rabbit populations (Faust et al.

2007). Hence, a severe grazing pressure is accompanied by a decrease in phytodiversity (Olsvig-Whittaker et al. 1993; Taddese et al. 2002).

Post-dispersal processes

Extensive livestock grazing can create gaps, which are favourable microsites for germination and the establishment of plants (Harper 1977; Green 1983). There are various types of gaps due to trampling activities, such as hoofprints, resting places or livestock trails, which are known to be important for the regeneration of plants or the maintenance of phytodiversity (Bakker & Olff 2003). This is especially the case regarding sand ecosystems (Jentsch 2004; Schwabe & Kratochwil 2004). Trampling processes of livestock like those known for sheep flocks can also facilitate the incorporation of epizoochorously dispersed seeds into soil substrate and therefore reduce the predation risk and stimulate the emergence of seedlings (Rotundo & Aguiar 2004; Eichberg et al. 2005). Accordingly, there were also several studies concerning the fate of endozoochorously dispersed seeds which showed that only a small proportion of viable seeds emerged under field conditions (e.g. Malo & Suárez 1995; Mouissie et al. 2005; Cosyns et al. 2006). Nevertheless, Eichberg et al. (2007) found mainly site-specific non-competitive species like annual herbs emerging out of sheep dung in inland sand ecosystems, even though there was a high seed potential of competitive species in the dung.

Thesis outline (see Figure 1.1)

The main part of this thesis deals with a successional gradient and the incorporated successional pathways with regard to different abiotic and biotic impacts (Chapters 2 & 3). Hence, in Chapter 2 the influence of varying nutrient additions on the vegetation of a low-productive and early-successional sandy grassland was investigated. I used an established nutrient addition experiment (Storm & Süss 2008) to analyse potential further changes regarding successional pathways and the speed of succession in this threatened community. Additionally, the impacts on phytodiversity, community and vegetation structure, different traits and plant functional types, phytomass production, individual plant species and endangered species were studied. This research was complemented with a seed limitation experiment by means of seed traps.

Chapter 3 examines the development of a threatened mid-successional sandy grassland in a long-term approach. Within 10 years the impact of different disturbance regimes concerning phytodiversity was analysed, including an extreme climatic event like the dry year in 2003 as an example for severe abiotic natural disturbances. The main focus was on the impact of extensive sheep grazing as a management measure for nature conservation purposes after a former mowing and mulching regime.

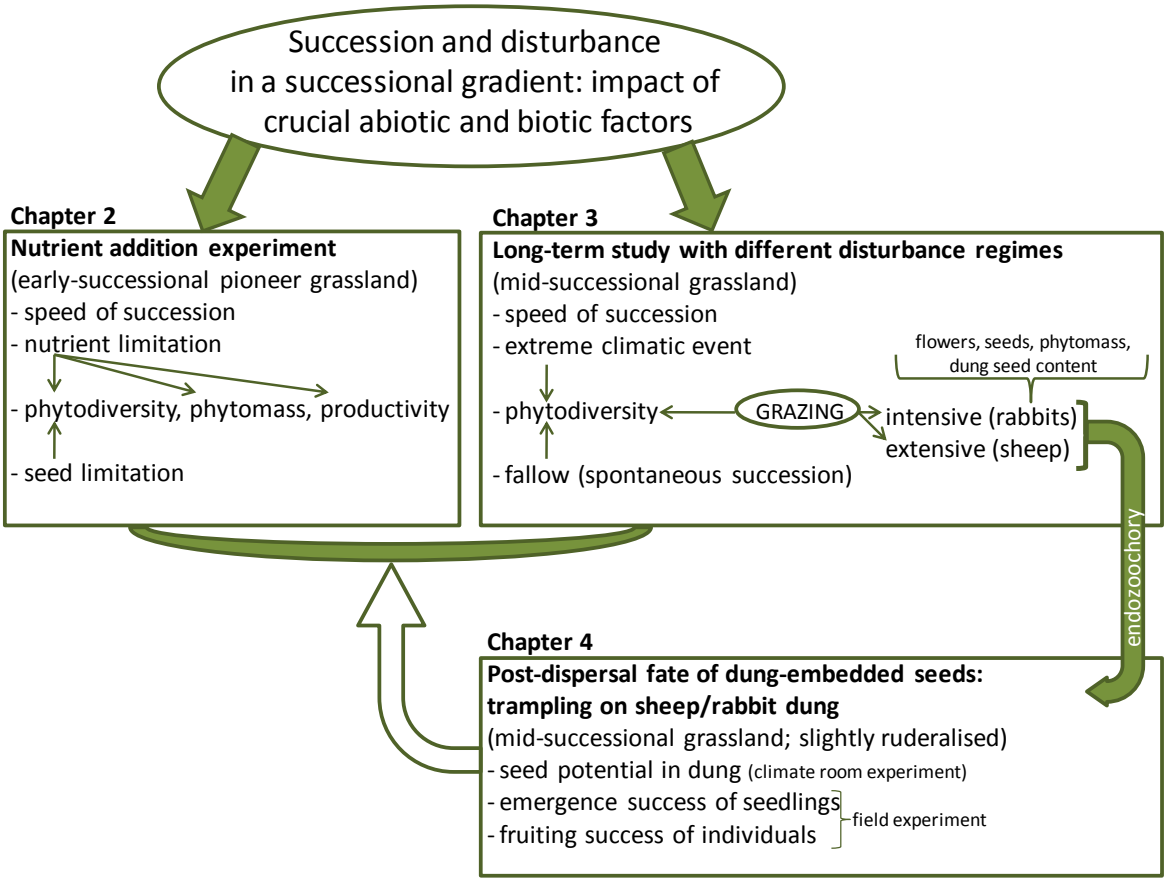

Figure 1.1: Flow diagram and interrelationship between the objectives of this thesis.

At the beginning of the study the influence of the local wild rabbit population could be neglected, but due to the strong increase in population densities I added a further investigation of the rabbits' impact on this threatened ecosystem. For this purpose, I analysed the flower production and phenology as well as the seed and phytomass production. An emergence experiment in a climate room should give information about the content of available seeds in rabbit dung. Another part of this study was the comparison of totally ungrazed plots (spontaneous succession) with the extensive sheep-grazing and intensive rabbit-grazing regimes. Accordingly, I tried to discriminate different succession lines. One of the central goals was to elucidate the response of the community in spite of different disturbance severities, and discover whether there is resistance, resilience or recovery or whether there is a breakdown of the whole community.

The successful dispersal and establishment of plants in fragmented landscapes is a crucial process within threatened communities. Therefore, in Chapter 4 the post-dispersal fate of dung-embedded seeds after endozoochorous transport was assessed. The use of large sheep flocks and the high population densities of rabbits lead to common trampling events on sheep and/or rabbit dung in our system. I expected that livestock trampling by sheep on dung pellets of both herbivore species would facilitate both the emergence and the establishment success of seedlings. As a reason,

the hard surface of the sheep pellets gets cracked if it is hit by a hoof. Subsequently, the cracked pellets were incorporated into the soil. For this experiment, which lasted two years, sheep and rabbit dung from a species-rich mid-successional Allio-Stipetum stand was collected, transferred to a slightly ruderalised mid-successional Armerio-Festucetum community which is dominated by competitive grasses, and dung pellets were cracked by means of a sheep-hoof replica. The seedling emergence and fruiting success of individuals was assessed and compared to that of intact pellets. Furthermore, the potential seed availability was studied in a preliminary experiment under optimised conditions in a climate room.

The results of all experiments are discussed in a synopsis in Chapter 5.

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2. Chapter 2 – Nutrient addition

Successional pathways under different nutrient regimes: lessons from threatened sandy grassland

Control plot with a low cover of phanerogams and a high cryptogam layer.

Plot with NPK treatment showing grass encroachment and a high vegetation density.

Abstract

Nutrient increase, e.g. by atmospheric nitrogen deposition or transfer of soil particles, is a major threat for many types of endangered open vegetation. As a model system we used threatened sandy grassland, where a nutrient addition experiment was started in the year 2000. We analysed the whole data set for a nine-year period and run extended approaches in the years 2007 to 2009. We added nitrogen in low dose to simulate an enhanced atmospheric deposition, nitrogen in high dose (N), nitrogen in high dose in combination with different micro- or macronutrients (NP, NPK, NPKM), phosphorus, and a carbon source to immobilise plant-available nitrogen to our experimental plots. Additionally, seed limitation was tested by assessing the local seed rain. The data set was analysed by means of detrended correspondence analysis (DCA) and linear mixed models.

The DCA revealed two successional pathways, a line, which is typical for threatened sandy grassland, and another one, which was accelerated and clearly separated from the typical one. These separations were only detectable after a "lag phase" of about five years. As a general trend phytodiversity diminished on all plots, but the decrease was significantly stronger on plots with high dose N, which have also shown higher turnover ratios. Site-specific species from pioneer stages (strategy type "stress-tolerators" and "ruderals") and "Red Data" species decreased with nutrient addition. Additionally, we observed an increase in cover of tall plants, geo- and hemicryptophytes, "competitors/stress-tolerators/ruderals" and competitive grasses on plots with high dose N. The above-ground phytomass production of phanerogams was up to 3-fold higher by N, NP, NPK or NPKM treatment, but it was significantly lower in the case of cryptogams. In contrast, low-dose nitrogen and phosphorus only had no impact with except for legumes, which were facilitated predominantly by P. The extended approach has shown that most plants were responsive to nutrient addition and grew taller or set more fruits respectively seeds. In the local seed rain many autochthonous and allochthonous species were found. Anyhow, most abundant species were non-target species and even *Calamagrostis epigejos* caryopses were found.

It could be shown, that the floristic structure, successional lines, phytodiversity and plant strategies of the studied system were changed after a five-year period and a threatened vegetation type was gradually replaced by one with dominant and/or competitive species. These findings emphasise the importance of long-term observations for the study of effects caused by nutrients.

Introduction

Nutrient limitation plays a crucial role in many natural and semi-natural terrestrial ecosystems. For example, nutrient status is the main factor affecting variation in European grassland vegetation (Havlová et al. 2004; Ellenberg & Leuschner 2010). In recent decades, many studies emphasised nitrogen as the main element limiting plant productivity (Janssens et al. 1998; Gough et al. 2000), but also the co-limitation of plant growth by nitrogen and phosphorus was highlighted (Willems et al. 1993; Morecroft et al. 1994; Wassen et al. 2005; Hejcman et al. 2007). If so, enhanced nitrogen availability, e.g. by long-term airborne nitrogen deposition, and/or phosphorus input by fertilisers can cause an increase in vegetation density, a loss in plant species richness and especially threaten endangered species (Schellberg et al. 1999; Gough et al. 2000; Shaver et al. 2001; Jacquemyn et al. 2003; Stevens et al. 2004; van der Hoek et al. 2004; Lanta et al. 2009). This is in strong accordance with observations in central and western European grasslands concerning the encroachment of grasses or the increase of ruderal species (Bobbink 1991; Bobbink et al. 1998; Carroll et al. 2003; Jentsch & Beyschlag 2003; Bakker 2005).

It has been proposed that constant but low-level nitrogen depositions have a greater impact on diversity than previously thought (Clark & Tilman 2008). In fact, long-term fertiliser application can create a shift towards plant communities belonging to different phytosociological classes (Chytrý et al. 2009). The floristic composition of species-rich grasslands is a result of and dependent on low soil fertility (Willems et al. 1993). Therefore, studies of nutrient limitations in natural and semi-natural grasslands are important and relevant for nature conservation. This applies especially to low-productive ecosystems such as threatened sandy pioneer grasslands. The atmospheric nitrogen depositions are often a larger source of plant nitrogen supply than mineralisation processes in the soil (Morecroft et al. 1994). Plant species adapted to infertile conditions can be systematically reduced by high nitrogen depositions (Stevens et al. 2004), which was also pointed out by Martensson & Olsson (2010) for sandy grasslands.

The species' response towards habitat changes like nitrogen inputs can depend on the community in which they live (Pennings et al. 2005) and the successional phase and therefore the competitive interactions in grassland vegetation (Hasse & Daniëls 2006). Hence, long-term observations are important and able to give valuable information about successional processes (Bakker et al. 1996; Schmidt et al. 2009; Süss et al. 2010). Regarding spontaneous succession in open pioneer grasslands, knowledge about successional processes and particularly the speed of succession is important and a primary concern.

Site characteristics are also closely related to species rarity; rare species often occur at warm, dry, light and nutrient-poor sites (Römermann et al. 2008). The threat is highest in early successional stages with small-growing and stress-adapted species. After nitrogen and/or phosphorus inputs, sand pioneer grassland can develop into vegetation with monodominant and competitive graminoids (Süss et al. 2010), which is also known for other open habitats (Kooijman & van der Meulen 1996; Dierschke 2006; Poschlod et al. 2009). Invasive and ruderal species, respectively, have in common that they are effective colonisers in the further succession due to their vegetative growth and propensity for lateral spread (Prach & Pyšek 1999; Kahmen & Poschlod 2004; Poschlod et al. 2009), and probably a higher reproductive potential by, e.g., comparatively long flowering periods (Cadotte et al. 2006) or better means of long-distance dispersal (Römermann et al. 2008).

Recently, many studies have dealt with nutrient application experiments in predominantly late-successional grasslands. Our study continues the nutrient addition experiment started by Storm & Süss (2008), which focuses on low-productive and species-rich pioneer stages in sand ecosystems with threatened vegetation of high nature-conservation value. This ecosystem type is inhabited by many endangered Red Data species (Petersen et al. 2003). The 5-year experiment of Storm & Süss (2008) showed the responsiveness of the examined plant community to nutrient addition and the nutrient limitation of most species of this pioneer grassland mostly regarding nitrogen and phosphorus. However, a change in phytodiversity was not observed by the authors, but accelerated succession. The present study continues this experiment for another four years.

The following questions were addressed:

1. Is the succession of pioneer grassland only accelerated by nutrient addition, or is there an alteration of successional lines?
2. Which plant functional types profit most from nutrient addition and what are their traits?
3. Are phytodiversity and threatened plant species negatively affected by the nine-year nutrient addition?

Methods

Study area

The study was carried out in Germany in the northern upper Rhine valley about 30 km south of Frankfurt/Main (Hesse) at the “Ehemaliger August Euler-Flugplatz von Darmstadt” (8°35’ E, 49°51’ N). The soil type is a calcaric Arenosol with silt + clay content < 10 %; further soil data from the studied area are given in Storm & Süss (2008). Organic carbon and total nitrogen content are very low. Mean annual

temperature is 11.1 ± 0.3 °C (mean ± SD; climate data from Deutscher Wetterdienst, Frankfurt/Main airport for the period 2000-2008) with an annual duration of sunshine of 1697 ± 190 h and a precipitation of 625 ± 133 mm yr^{-1}. In 2000, 2002 and 2003, annual temperature was above average. The duration of sunshine in the extraordinary year 2003 was high (2138 h) and the precipitation was very low (379 mm yr^{-1}).

The investigated vegetation type can be classified as early successional stages of Koelerion glaucae (Koelerio-Corynephoretea), "grasslands of stable neutral sandy soils in central and northeastern Europe" (29D01 according to ETC/BD 2008), which is of high nature-conservation value and protected by the European Fauna-Flora-Habitat directive (Natura 2000-Code 6120; Ssymank et al. 1998). The whole area has been managed by grazing with sheep and donkeys since 1999 with the exception of experimental plots.

Experimental design

In 2000, five blocks were established in a randomised block design, each block containing eight plot types (each plot 11.56 m^2). Plots are separated from each other by 50 cm wide buffering stripes. Every plot is divided into a permanent plot of 4 m^2 for vegetation recordings and the remaining peripheral plot area is designated for a yearly phytomass sampling. Blocks are protected against sheep, donkeys and rabbits by fencing.

Table 2.1: Applied nutrients and doses.

Treatment	Treatment group	Element	Chemical formula	Dose (kg element ha^{-1} yr^{-1})
0 (Control)	N–	-	-	-
C	N–	C	$C_{12}H_{22}O_{11}$ (Sucrose)	547
		C	Sawdust	145
P	N–	P	$NaH_2PO_4*2H_2O$	50
n	N–	N	NH_4NO_3	25
N	N+	N	NH_4NO_3	100
NP	N+	N	NH_4NO_3	100
		P	$NaH_2PO_4*2H_2O$	50
NPK	N+	N	NH_4NO_3	100
		P	$NaH_2PO_4*2H_2O$	50
		K	KCl	60
NPKM	N+	N	NH_4NO_3	100
		P	$NaH_2PO_4*2H_2O$	50
		K	KCl	60
		Mg	$MgSO_4*7H_2O$	52
		Fe	$FeC_6H_5O_7*5H_2O$	13
		B	$Na_2B_4O_7*10H_2O$	2.72
		Mn	$MnSO_4*H_2O$	13.23
		Zn	$ZnSO_4*7H_2O$	0.23
		Cu	$CuSO_4*5H_2O$	0.25
		Mo	$(NH_4)_6Mo_7O_{24}*4H_2O$	0.54

Applied nutrients and doses for the different treatments are shown in Tab. 2.1. The composition of nutrient solutions complies largely with Atkinson (1973). For restoration purposes in open sandy grasslands, Török et al. (2000) suggested the input of organic carbon (e.g. sawdust and saccharose) to stimulate microbial biomass and immobilise soil nitrogen.

To simulate atmospheric nitrogen deposition, N was applied at a low dose ("n") of 25 kg $ha^{-1}yr^{-1}$, and at a high dose ("N") of 100 kg $ha^{-1}yr^{-1}$ to test N-limitation. Nutrients were applied dissolved in tap water ten times a year except for sawdust, which was spread once a year.

Nitrogen deposition

The airborne nitrogen deposition at our study site was assessed in one- (maximum temperature of the day > 15 °C) respectively two week-intervals (temperature < 15 °C) by means of three bulk collectors, which were installed in three of the experimental blocks between January 2009 and January 2010. The collectors were protected against defecation of resting birds with wired spikes. We analysed nitrate and ammonium concentrations photometrically. Additionally, the amount of precipitation, pH-values and conductivity were analysed. Samples which were obviously contaminated by bird faeces or insects (sample was murky or with suspended particles, or conductivity was notably higher), had to be dismissed for the final calculations. In total, 220 samples were tested and 95 of them were supplemented by mean annual data because of missing values. The total nitrogen deposition was calculated by including the wet and dry nitrogen deposition with the use of conversion factors (Gauger et al. 2000). Accordingly, we added a dry deposition of about 113 % to our wet-only values (see Bergmann 2004).

Vegetation relevés

The percentage cover of vascular plants, bryophytes and lichens on the permanent plots was estimated twice a year in May/June and in September on a redefined Londo (1976) scale (<1/1/2/3/ … /8/9/10/15/20/ … /95/100 %), the first relevés took place in September 2000 (Bergmann 2004). We combined relevés of autumn and the following spring into one annual vegetation relevé by using the maximum values for each plant species. Since 2005/06, the cover of bryophytes was divided into living and dead bryophytes and estimated separately. In addition, the cover of litter was estimated since 2005. For this thesis the relevés were estimated from 2006/07 to 2008/09.

We analysed the cover values of plant functional types (PFTs) “graminoids”, “herbs”, “cryptogams” (bryophytes + lichens), “bryophytes”, “lichens”, “legumes” (Fabaceae) and “competitive graminoids” (*Agrostis capillaris*, *Calamagrostis epigejos*, *Carex hirta*, *Cynodon dactylon*, *Elymus repens* and *Poa angustifolia*) between 2000/01 and 2008/09 and the cover of “dead bryophytes” and “litter” between 2005/06 and 2008/09. The species composition was analysed in the same time frame by means of the total species number (phytodiversity) and the number of PFTs (for description of PFTs see above). Additionally, the following parameters were tested: ecological strategy type (according to Grime 1979); morphology traits: growth height (based upon observations in the field: GH1 = 0-20 cm; GH2 = 21-50 cm; GH3 > 50 cm), life span (annual, biennial, perennial), life form (chamaephyte, geophyte, hemicryptophyte, therophyte); reproduction type (s, by seed; v, vegetatively; sv, by seed and vegetatively; ssv, mostly by seed; vvs, mostly vegetatively); seed bank type (transient, persistent); seed weight; turnover ratio (defined as the quantity (%) of

plant species which was exchanged between two consecutive years); target species ratio (TSR, Eichberg et al. 2010); "Red Data" species (Germany; Ludwig & Schnittler 1996) and Ellenberg indicator values (nitrogen, moisture; both weighted and unweighted; Ellenberg et al. 2001). Tests were carried out quantitatively (cover sum) as well as qualitatively (species number) when possible.

Data were included from the sources BIOLFLOR (Klotz et al. 2002), LEDA Traitbase (Kleyer et al. 2008) and Seed Information Database (SID, Royal Botanic Gardens Kew 2008). Nomenclature follows Wisskirchen & Haeupler (1998) for vascular plants, Koperski et al. (2000) for bryophytes, Scholz (2000) for lichens and Oberdorfer (2001) for plant communities.

Phytomass

The phytomass was sampled every year in September (peak standing crop) from 2000 to 2008 by the use of six randomly chosen subplots of 400 cm^2 for each treatment plot. After clipping to ground (including standing dead), the above-ground phytomass was separated into the litter and the PFTs "graminoids and herbs", "legumes" and "cryptogams", bulked together for each plot. Since 2006, analysis of the phytomass of "cryptogams" has also been further differentiated by a separation into "bryophytes" and "lichens". The below-ground phytomass ("roots") was sampled up to a soil depth of 30 cm with a liner sampler (4.7 cm diameter) and sieved (mesh width 0.71 mm). Samples were oven dried for 48 h at 70 °C and weighed afterwards.

Extended approach and seed rain

Within the years 2004-2009, additional parameters such as growth height, number of individuals and fecundity (fruit/seed production per individual), concerning early- and mid-successional single species with a sufficient frequency on the plots, were analysed for single or several years. For this purpose, at least ten randomly chosen individuals per treatment plot were used. Data from 2004 were provided by Karin Süss, from 2005 and 2006 by Faust (2006) and data from 2007 to 2009 by this study.

The following species were analysed regarding their growth height (investigated years in brackets): *Bromus tectorum* (2006), *Centaurea stoebe* s.l. (2005-2007), *Cerastium semidecandrum* (2007), *Erophila verna* (2007), *Medicago minima* (2006), *Phleum arenarium* (2005, 2006, 2008), *Saxifraga tridactylites* (2005-2007), *Silene conica* (2005, 2006), *Silene otites* (2008) and *Veronica praecox* (2009); regarding the number of individuals: *Centaurea stoebe* s.l. (flowering individuals; 2005), *Medicago minima* (2005), *Silene conica* (2005, 2006) and *Veronica praecox* (2008, 2009);

regarding fecundity parameters: *Centaurea stoebe* s.l. (achenes, 2007), *Cerastium semidecandrum* (capsules + seeds, 2007), *Saxifraga tridactylites* (capsules, 2005-2007; seeds, 2007), *Silene conica* (capsules, 2004-2006) and *Veronica praecox* (capsules, 2008).

To assess the seed rain we installed between November 2008 and December 2009 fifty funnel traps (0.452 m^2 capturing size each; 10 per block; after Kollmann & Goetze 1998). To prevent defecation of resting birds into the funnels we protected the upper funnel edge with wired spikes. Trapped seeds were collected every two weeks, identified with the help of a reference collection as well as determination literature (Beijerinck 1976; Cappers et al. 2006) and counted subsequently.

Statistical analyses

The composition of the community (cover values) was analysed with detrended correspondence analysis (DCA) using PC-ORD 5.31 (MjM Software, Gleneden Beach, OR, USA). Means of the root transformed cover values were used and the analysis was run using the options downweighting and rescaling; the number of segments was 26.

The effects of the variables "treatment" and "year" on the dependent variables were analysed by calculating mixed linear models (SAS 9.2 PROC GLIMMIX, SAS Institute Inc., Cary, NC, USA), which are especially suitable for analyzing repeated-measures data (Littell et al. 1998, 2000). We compared 14 covariance structures (e.g., autoregressive, compound symmetry, unstructured, autoregressive heterogeneous, compound symmetry heterogeneous, autoregressive moving-average, Toeplitz and Huynh-Feldt) according to the corrected Akaike criterion (AICC) (Fernández 2007). If two structures led to equal AICC values, the simpler structure was chosen. For the calculation of degrees of freedom, we selected the Kenward-Roger approximation. The studentised residuals and conditional studentised residuals were examined for normality by means of graphical display (histograms and quantile-residuum plots); nearly Gaussian distributions could be ascertained.

In a first step, plots from the reference year 2000 were checked for no initial differences between the plots before treatments began. Dunnet-adjusted tests were conducted to compare each treatment to the control group using the LSMEANS procedure of PROC GLIMMIX subsequently. There were nearly no significant treatment effects among the control (0), C, P and n treatments, but the four treatments with nitrogen in high dosages (N, NP, NPK, NPM) were effective very similarly. Therefore, treatments were pooled into two treatment groups (N– = without N in high dosage, N+ = with N in high dosage) for further analyses using the ESTIMATE procedure of PROC GLIMMIX. The year 2000 was used as covariate for every following year applying the "baseline" option of PROC GLIMMIX. Tukey-adjusted post-hoc tests were carried out to determine in which years the two

treatment groups differed from each other significantly. Significance was set at a level of $p < 0.05$.

In the "Results" section only significantly influenced parameters are mentioned.

Results

Airborne nitrogen deposition

The total airborne nitrogen deposition including wet and dry deposition at our experimental site in 2009 was about 17.2 kg $ha^{-1}yr^{-1}$.

Community composition

Community composition and the temporal trajectories of the plots are depicted in Fig. 2.1 by means of detrended correspondence analysis (DCA). It is shown that the plots in 2000/01 and 2001/02 are hardly separated, but afterwards the trajectories of all plot types point towards the right side, indicating the same general successional trend. All plots show very long trajectories between the years 2001/02 and 2002/03, indicating the influence of the dry year 2003. The development of plots with nitrogen in low doses ("n") was similar to that of other plot types without any nitrogen addition (control, C, P). However, all plots with high-dose N are separated along the second axis and the two treatment groups diverge from each other especially after the years 2003/04 and 2004/05. The distance between these treatment groups is evident for an accelerated speed of succession of plots with N and predominantly with NP, NPK or NPKM treatment. Especially after 2007/08 trajectories of the high-dose N treatments changed their direction and are pointing downwards in the diagram. Besides, among the N– treatment group the carbon plots (C) moved furthest pointing upwards, showing the greatest distance from the plots with combinations of N and P treatments.

The following species showed a decrease in cover during succession (strong negative correlation with axis 1; $r < -0.3$): *Arabidopsis thaliana*, *Armeria maritima* ssp. *elongata, Brachythecium albicans*, *Bromus sterilis*, *Bryum caespiticium*, *Conyza canadensis*, *Corynephorus canescens*, *Geranium molle*, *Helichrysum arenarium*, *Hypericum perforatum*, *Hypnum lacunosum*, *Medicago minima*, *Myosotis ramosissima*, *M. stricta*, *Koeleria glauca*, *Oenothera biennis* s.l., *Peltigera rufescens*, *Petrorhagia prolifera*, *Psyllium arenarium*, *Saxifraga tridactylites*, *Sedum acre*, *Tortula ruraliformis*, *Trifolium arvense*, *Trifolium campestre*, *Vicia lathyroides* and *Vulpia myuros*.

The following species showed an increase in cover during succession (strong positive correlation with axis 1; $r > 0.3$): *Asparagus officinalis*, *Carex hirta*, *Centaurea*

stoebe s.l., *Cladonia furcata*, *C. pyxidata* (incl. *C. rei*), *C. rangiformis*, *Elymus repens*, *Poa angustifolia*, *Silene otites*, *Stipa capillata* and *Verbascum phlomoides*.

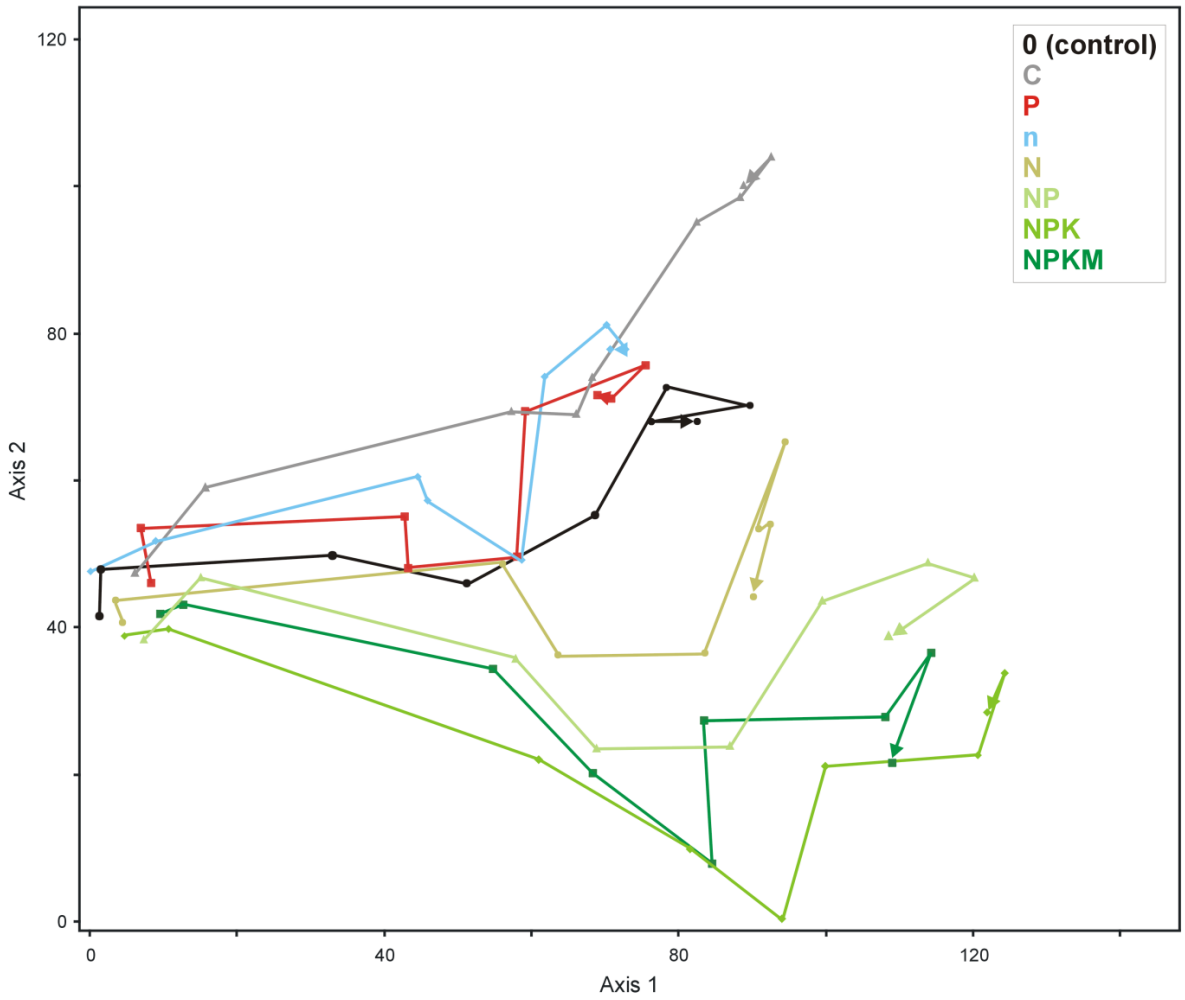

Figure 2.1: Trajectories of the treatment plots (DCA) between 2000/01 and 2008/09. Treatment is indicated by different colours, years by time points. The time points of each plot type have been connected by trajectories. Eigenvalues: axis 1: 0.12, axis 2: 0.05, axis 3: 0.03. Axes are scaled in 1 SD = 100.

The nutrient gradient along the second axis is represented by many species, which showed an increase in cover on high-dose N plots (lower part of the diagram, negative correlation with axis 2; $r < -0.3$): *Agrostis capillaris*, *Bromus tectorum*, *Carex hirta*, *Carex praecox*, *Cerastium semidecandrum*, *Chenopodium album* agg., *Cynodon dactylon*, *Elymus repens*, *Erodium cicutarium* agg., *Fallopia convolvulus*, *Geranium molle*, *Hypericum perforatum*, *Phleum phleoides*, *Poa angustifolia*, *Sedum acre*, *Senecio vernalis*, *Sisymbrium altissimum* and *Veronica arvensis*.

Conversely, the following species were positively correlated with axis 2 ($r > 0.3$) and showed higher cover values on plots without high dose N treatment (upper part of the diagram): *Artemisia campestris*, *Cetraria aculeata*, *Cladonia furcata*, *Cladonia pyxidata* (incl. *C. rei*), *Hieracium pilosella*, *Hypochaeris radicata*, *Koeleria macrantha*,

Medicago falcata (incl. *M.* x *varia*), *Silene otites*, *Thymus pulegioides*, *Veronica praecox* and *Vicia angustifolia*.

The turnover ratio in Fig. 2.2a indicates significant differences concerning the treatment groups and individual treatments (Tab. 2.2), showing a significant effect of the treatments N, NP, NPK and NPKM. The species turnover within the N+ group was higher in many years, exhibiting two peaks, one between the years 2001/02 and 2002/03, and another one between the years 2005/06 and 2006/07, each peak with a species turnover of 30-35 %. Prior to this time span, in 2000/01, the turnover ratio was only 15 %, much lower than the subsequent peaks in both treatment groups. Tukey-adjusted post-hoc tests revealed significant differences between treatment groups in 2002/03 and since 2004/05 (Tab. 2.2).

Species composition

Phytodiversity was high in 2000/01 and 2001/02, with about 26 phanerogam species and 5 cryptogam species on the control plots (Fig. 2.2b). As a general trend, species numbers were lower since the dry year 2002/03 concerning the control and all other treatments. Therefore, statistical tests did not reveal any significant effects of individual treatments, but years and also treatment groups differed highly significantly (Tab. 2.2). Since 2005/06 phytodiversity of the N+ group was significantly lower than in the N– group.

By contrast, the number of lichen species slightly increased in both treatment groups after 2003/04 (Fig. 2.2c) but the increase was higher in the N– group and the two groups differed significantly since 2005/06 (Tab. 2.2). However, N, NP and NPK treatment led to a significant decline of legume species. Pooling into treatment groups could demonstrate a decline of legumes in the N+ group especially between 2005/06 and 2007/08 (Fig. 2.2d). Post-hoc tests showed differences of treatment groups in 2004/05, 2005/06, 2007/08 and 2008/09. The number of graminoids or herbs was neither significantly affected by a general treatment nor by treatment groups, but showed an effect of the factor year. Nevertheless, there was a trend showing differences between treatment groups in the later years of the investigation, indicating a depression in the N+ group (Tab. 2.2).

The number of stress-tolerating species (strategy type “s”) was very low in the field (only *Sedum acre* and *Silene otites*). Therefore, we pooled them with the stress-tolerators/ruderals (“sr”) before analysing. NP, NPK and NPKM treatments significantly decreased the number of species of the combined strategy type “s/sr”, while it was nearly identical in the N+ and the N– group during the first five years (Fig. 2.3a), after which the number of these species decreased in the N+ group, and post-hoc tests showed significant differences between the two groups since 2005/06 (Tab. 2.2). The number of “r” strategists was significantly affected by even all treatments containing nitrogen (including low doses): first, they showed a slight

increase, but afterwards they declined. Thus treatment groups differed in 2003/04 and since 2006/07 (Tab. 2.2). Similar to the former strategy type, ruderals predominantly decreased in the N+ group, which is depicted in Fig. 2.3b.

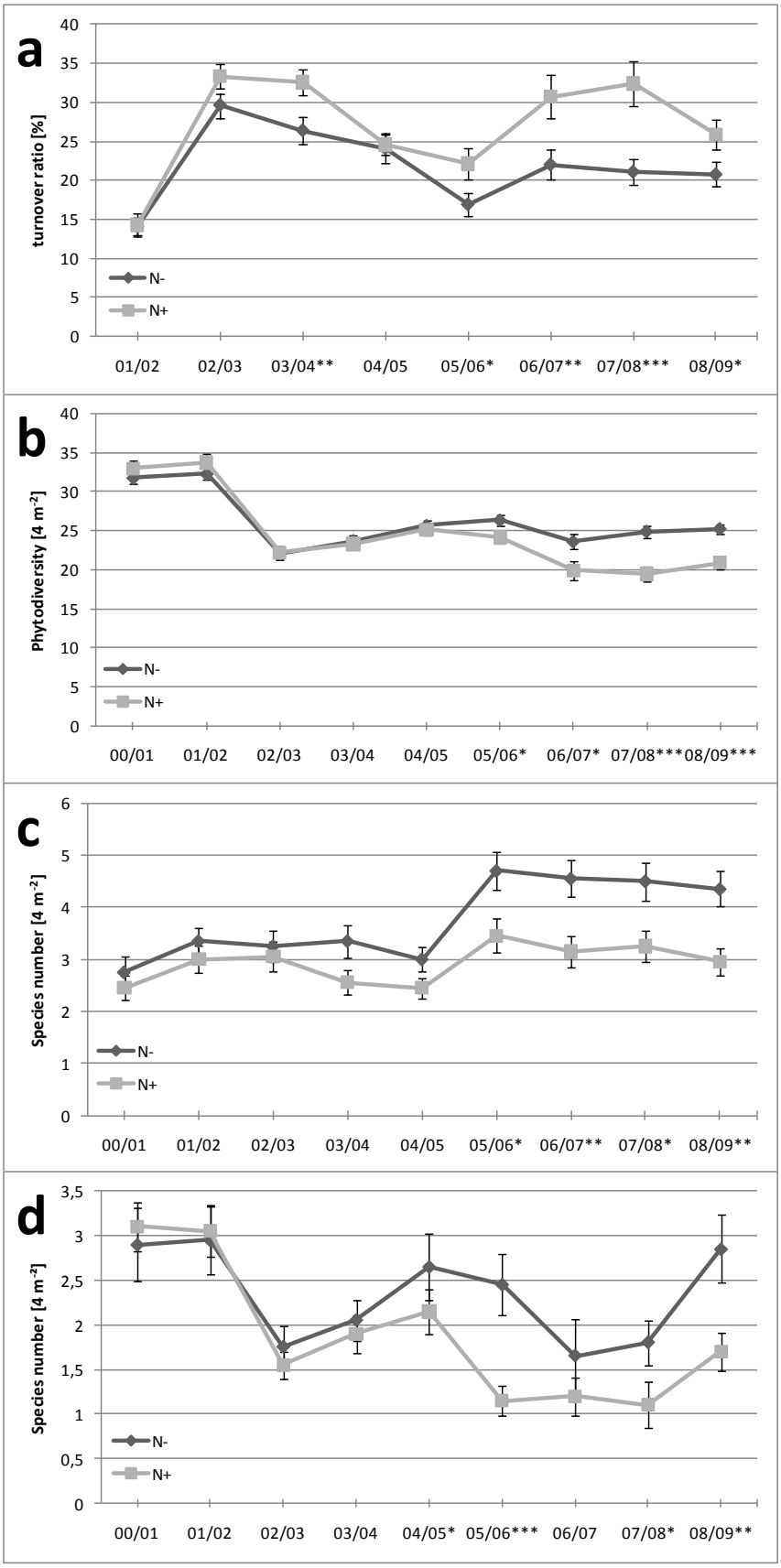

Figure 2.2: Turnover ratio, phytodiversity and species numbers of plant functional types after pooling into treatment groups. a. Turnover ratio between two years; b. Phytodiversity (total species number); c. Lichens; d. Legumes. Years with significant differences between N– and N+ treatment groups are marked * at the x-axis labels.
Error bars = standard error.

Table 2.2: Results of the mixed linear models of the turnover ratio, Ellenberg N values, target species ratio and species numbers of different parameters for the years 2001-2008. The first section describes a model for the eight individual treatments, the second section a model for the two treatment groups N+/N– after pooling. Figures <1 in the 'Ratio' column indicate depression by high-dosage N. The ratio was calculated using mean values of the examined years of both treatment groups. Significant results are shown (in bold print); *p* = level of significance.

	Treatment	Year	Treatment *year	Treatment group	Ratio N+:N– group	Treatment group*year1	Treatment group*year2	Treatment group*year3	Treatment group*year4	Treatment group*year5	Treatment group*year6	Treatment group*year7	Treatment group*year8
Variable	*p*	*p*	*p*	*p*		*p*	*p*	*p*	*p*	*p*	*p*	*p*	*p*
Turnover ratio	**0.0001**	**<0.0001**	0.0849	**<0.0001**	1.2	0.9105	0.0863	**0.0041**	0.8118	**0.0217**	**0.002**	**<0.0001**	**0.0229**
Ellenberg N													
weighted	0.0896	**<0.0001**	0.9392	**0.0246**	1.1	0.8236	0.6217	0.2735	0.0803	**0.0122**	**0.0203**	0.2232	**0.0097**
unweighted	0.2130	**<0.0001**	0.7635	**0.0298**	1.1	0.6827	0.3959	0.3724	0.1434	**0.0051**	0.1882	**0.0116**	0.0840
TSR_{qual}	0.0973	**<0.0001**	0.7266	**0.0223**	0.9	0.6351	0.3948	0.4298	0.0595	**0.0078**	**0.0215**	0.0504	0.2209
Species number													
Total (Phytodiversity)	0.1943	**<0.0001**	0.4495	**0.0091**	0.9	0.6973	0.9880	0.6164	0.4333	**0.0496**	**0.0145**	**0.0004**	**0.0009**
Graminoids	0.6555	**<0.0001**	0.2389	0.0637	1.0	0.5355	0.8389	0.5999	0.1305	0.4168	**0.0116**	**0.0009**	**0.0290**
Herbs	0.2973	**<0.0001**	0.6197	0.0615	0.9	0.6403	0.7104	0.9967	0.9801	0.1196	0.0786	**0.0060**	**0.0225**
Lichens	0.3614	**<0.0001**	0.1839	**0.0153**	0.8	0.5791	0.9375	0.0843	0.1383	**0.0118**	**0.0038**	**0.0124**	**0.0016**
Legumes	**0.0208**	**<0.0001**	0.4767	**0.0020**	0.8	0.7960	0.3080	0.2515	**0.0432**	**<0.0001**	0.0824	**0.0251**	**0.0010**
Strategy typ 's/sr'	**0.0196**	**<0.0001**	0.3765	**0.0042**	0.9	0.5509	0.9969	0.9638	0.7145	**0.0147**	**0.0031**	**0.0002**	**0.0008**
Strategy typ 'r'	**0.0105**	**<0.0001**	0.1549	0.3237	1.0	0.9027	0.9827	**0.0187**	0.1497	0.2680	**0.0115**	**0.0021**	**0.0305**
"Red Data" species	**0.0159**	**<0.0001**	0.1484	**0.0018**	0.8	0.9437	0.8882	0.4344	0.1218	**0.0043**	**0.0002**	**<0.0001**	**<0.0001**

There was a significant negative influence of N, NP, NPK and NPKM treatments on "Red Data" species (phanerogams and cryptogams; Tab. 2.2). Species numbers of the N+ treatment group declined from 10 species in 2000/01 to six species in 2008/09 (Fig. 2.3c). "Red Data" species of the N– treatment group almost remained at the same level throughout the years or even increased by about 1-2 species. Both N+ and N– groups differed significantly from each other since 2005/06 (Tab. 2.2).

Cover of plant functional types, single plant species and additional parameters

Nearly all analysed vegetation layers or additional parameters were highly significantly influenced by the factor year or by treatment groups (Tab. 2.2, 2.3).

All four treatments with N in high doses significantly raised the cover of herbs; the cover of dead bryophytes was enhanced by NPK and NPKM treatment only, whereas the interaction term "treatment*year" significantly affected the cover of bryophytes (Tab. 2.3). There was a strong increase of the cover of herbs since 2003/04 regarding both treatment groups but values of the N+ group were always higher and remained at a higher level (Fig. 2.4a). Treatment groups differed always significantly after 2000/01 (Tab. 2.3). The amount of dead bryophytes was significantly higher in the N– group in 2005/06 (Tab. 2.3) but decreased in both treatment groups afterwards and reached the same level by 2008/09. Concerning bryophytes, the decrease of cover values of the N+ group was stronger and Tukey-adjusted post-hoc tests revealed significant differences of both treatment groups in 2003/04, 2004/05,

2007/08 and 2008/09 (Fig. 2.4b, Tab. 2.3). Competitive graminoids were significantly affected by treatment group (Tab. 2.3). Cover values of the N– group only slightly increased throughout the years, but in 2008/09, values of the N+ group were about 5-fold higher than in 2000/01 (Fig. 2.4c). Cover values of non-competitive graminoids (not depicted) like *Corynephorus canescens*, *Koeleria glauca* or *Phleum arenarium* decreased during the years without dependence on the treatment group.

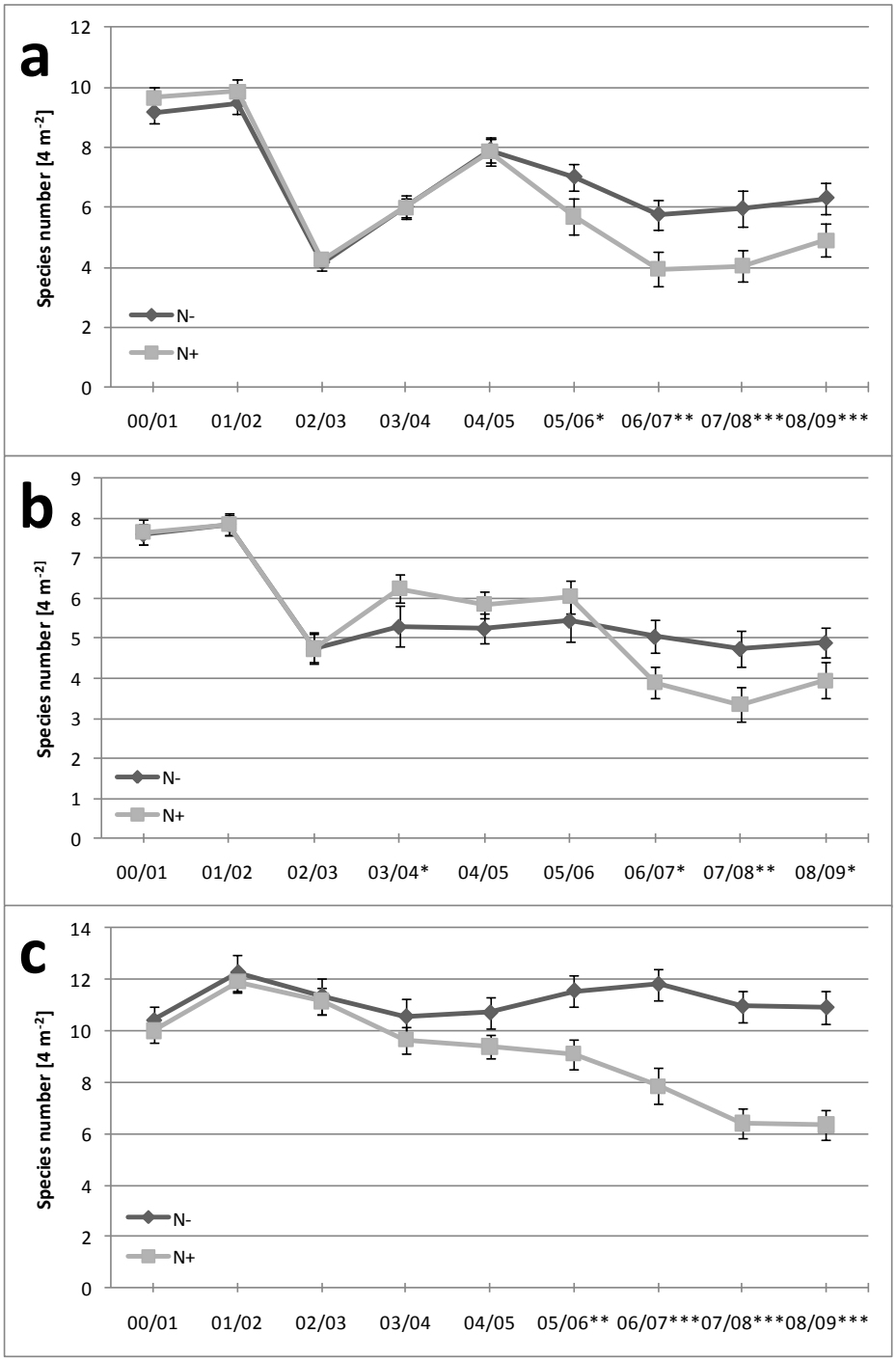

Figure 2.3: Species numbers of ecological strategy types and "Red Data" species after pooling into treatment groups. a. Strategy type "s/sr"; b. Strategy type "r"; c. "Red Data" species. Years with significant differences between N– and N+ treatment groups are marked * at the x-axis labels. Error bars = standard error.

Table 2.3: Results of the mixed linear models of the cover of different analysed variables, the cover of individual species and phytomasses. The first section describes a model for the eight individual treatments, the second section a model for the two treatment groups N+/N– after pooling. Figures <1 in the 'Ratio' column indicate depression by high-dosage N. The ratio was calculated using mean values of the examined years of both treatment groups. Significant results are shown (in bold print); p = level of significance.

	Treatment		Year		Treatment *Year		Treatment group		Ratio N+:N– group	Treatment group*Year1		Treatment group*Year2		Treatment group*Year3		Treatment group*Year4		Treatment group*Year5		Treatment group*Year6		Treatment group*Year7		Treatment group*Year8	
Variables	p		p		p		p			p		p		p		p		p		p		p		p	
Cover of PFTs, traits etc.																									
Herbs	**0.0007**		**<0.0001**		0.9608		**<0.0001**		1.7	**0.0012**		**0.0059**		**<0.0001**		**<0.0001**		**0.0005**		**0.0015**		**0.0010**		**0.0093**	
Bryophytes	0.0594		**<0.0001**		**0.0003**		**0.0031**		0.8	0.4196		0.4649		**0.0042**		**0.0001**		0.1097		0.0525		**0.0019**		**0.0006**	
Competitive graminoids	0.3748		**0.0057**		0.8209		**0.0173**		3.3	0.3731		**0.0105**		0.0586		**0.0408**		0.0590		**0.0204**		**0.0177**		**0.0229**	
Litter	0.0639		**0.0048**		0.8091		**0.0010**		2.3									**0.0011**		**0.0009**		**0.0002**		**0.0179**	
Dead bryophytes	**0.0114**		**<0.0001**		0.0869		0.1060		0.6									**0.0145**		0.1491		0.2595		0.8838	
Growth height 3	**0.0071**		**<0.0001**		0.2457		**<0.0001**		2.4	0.7878		0.1405		**0.0062**		**0.0008**		**0.0011**		**0.0033**		**0.0002**		**<0.0001**	
Strategy type 'csr'	**0.0107**		**<0.0001**		0.6747		**0.0001**		2.0	0.0515		**0.0053**		0.0745		**0.0091**		**0.0032**		**0.0004**		**0.0023**		**0.0050**	
Geophytes	0.5551		**0.0263**		0.5631		**0.0325**		3.4	0.7596		0.2764		0.5987		0.1435		0.1136		**0.0440**		0.0585		0.0546	
Hemicryptophytes	**0.0029**		**<0.0001**		0.9959		**<0.0001**		1.7	**0.0051**		**0.0011**		0.0516		**0.0387**		**0.0119**		**0.0007**		**0.0001**		**0.0010**	
Seed bank transient	**<0.0001**		**<0.0001**		0.0519		**<0.0001**		1.9	**0.0029**		**0.0254**		**<0.0001**		**<0.0001**		**<0.0001**		**<0.0001**		**<0.0001**		**<0.0001**	
Seed bank persistent	**0.0464**		**<0.0001**		0.4452		**0.0306**		1.5	**0.0175**		**0.0038**		**0.0127**		0.1435		0.5854		0.2582		0.4640		0.4188	
Reproduction type 's/ssv'	**<0.0001**		**<0.0001**		0.6688		**<0.0001**		1.7	**0.0024**		**0.0118**		**<0.0001**		**0.0006**		**<0.0001**		**0.0043**		**0.0333**		**0.0083**	
Reproduction type 'sv'	0.1871		**0.0005**		0.1122		**0.0193**		1.9	0.1142		**0.0049**		0.2552		0.5300		0.5064		0.0644		0.0606		**0.0193**	
Reproduction type 'v/vvs'	0.0646		**0.0067**		0.2516		**0.0208**		2.5	0.0986		**0.0304**		**0.0240**		**0.0437**		0.2683		**0.0482**		**0.0109**		0.1887	
"Red Data" species (phanerogams)	**0.0427**		**<0.0001**		0.5387		**0.3193**		0.9	0.1788		0.3447		0.3830		0.4956		**0.0235**		0.0881		**0.0091**		**0.0073**	
Cover of individuals																									
Bromus tectorum	**0.0192**		**<0.0001**		**0.0076**		**0.0009**		3.5	0.1109		**0.0012**		**0.0010**		**0.0249**		**0.0483**		0.1253		0.5467		0.4477	
Centaurea stoebe s.l.	0.0617		**<0.0001**		0.2308		**0.0007**		2.4	0.8058		0.0620		**0.0101**		**0.0013**		**0.0016**		**0.0022**		**0.0037**		**0.0075**	
Cetraria aculeata	0.1055		**0.0218**		0.1452		**0.0082**		0.1	0.2645		0.2602		0.0911		0.0685		**0.0297**		**0.0291**		**0.0423**		0.0861	
Medicago minima	**<0.0001**		**<0.0001**		**0.0037**		**0.0378**		0.6	0.6073		0.0521		0.0733		0.8143		0.3396		0.2807		**0.0033**		**0.0154**	
Verbascum phlomoides	0.1360		0.0785		0.8162		**0.0120**		6.3	0.8795		0.2730		0.5682		0.1478		0.0689		0.2401		0.1897		**0.0207**	
Phytomass																									
Phanerogams	**0.0002**		**<0.0001**		0.6668		**<0.0001**		1.8	**0.0133**		**0.0032**		**0.0064**		**<0.0001**		**<0.0001**		**0.0140**		**<0.0001**		**0.0008**	
Cryptogams	**<0.0001**		**<0.0001**		0.1493		**<0.0001**		0.8	0.7163		0.4226		**0.0005**		**0.0001**		**0.0277**		**0.0013**		**<0.0001**		**<0.0001**	
Roots	0.6186		**0.0004**		0.8029		0.0564		1.5	0.3807		0.6291		0.0630		0.1223		0.4589		**0.0097**		0.2696		**0.0085**	
Litter	**<0.0001**		**<0.0001**		0.0567		**<0.0001**		2.0	0.8967		0.3305		**0.0001**		**0.0246**		**<0.0001**		**<0.0001**		**<0.0001**		**0.0123**	
Bryophytes	**<0.0001**		**0.0274**		**0.0380**		**<0.0001**		0.6											**0.0006**		**<0.0001**		**<0.0001**	
Lichens	0.8326		**0.0021**		0.5091		0.9193		1.0											0.9725		0.8585		0.7484	

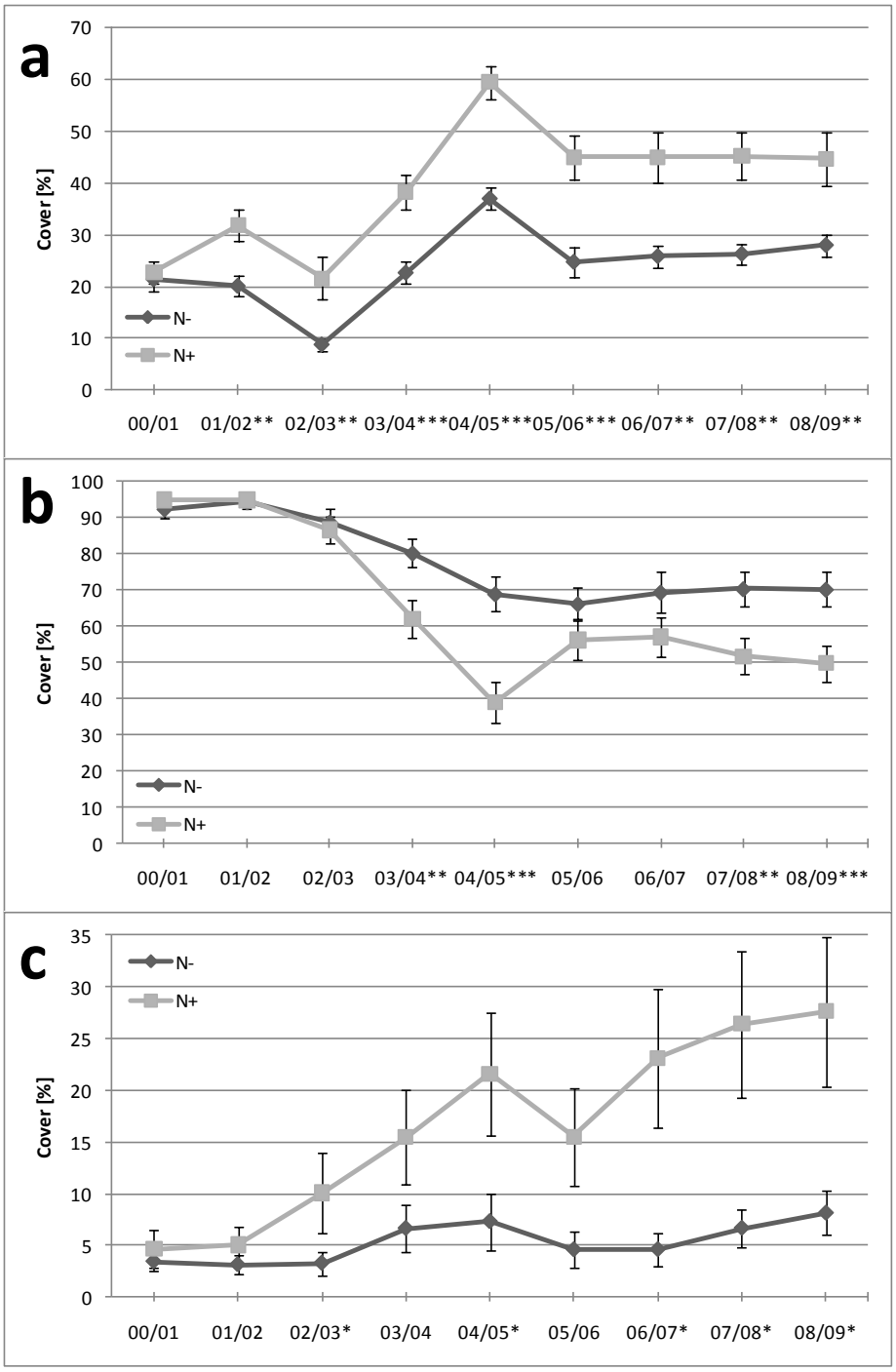

Figure 2.4: Cover of plant functional types after pooling into treatment groups. a. Herbs; b. Bryophytes; c. Competitive graminoids. Years with significant differences between N– and N+ treatment groups are marked * at the x-axis labels. Error bars = standard error.

Concerning morphology traits, the cover of tall plants (GH3; > 50 cm) was significantly increased by NP, NPK and NPKM treatment (Tab. 2.3), which resulted in higher cover values among the N+ group (4-5-fold increase), as shown in Fig. 2.5a. Treatment groups differed significantly since 2003/04 (Tab. 2.3). The life forms geophytes and hemicryptophytes profited significantly by NP, NPK and NPKM treatments, evident also in treatment-groups (Tab. 2.3), and cover values of the N+ group increased (Fig. 2.5b,c). Differences between the treatment groups regarding hemicryptophytes were identified by the use of post-hoc tests in the years 2001/02

and 2002/03 and since 2004/05 (Tab. 2.3). Treatment groups of geophytes differed significantly only in 2006/07. The following years were slightly not significant.

Plant species of the "csr" strategy type showed an up to 8-fold increase in cover values with high-dose N (Fig. 2.5d). These strategists profited significantly by NP, NPK and NPKM treatments and treatment groups were significantly different from each other in 2002/03 and since 2004/05 (Tab. 2.3).

Treatments significantly affected the cover of plants with a persistent seed bank type (treatments NP and NPKM) as well as plants with a transient one (treatments N, NP, NPK and NPKM), but effects were more pronounced concerning the latter type (Tab. 2.3; Fig. 2.5e,f). As the diagram with both treatment groups in Fig. 2.5e shows, most analysed plant species possess a transient seed bank and cover values increase in both groups, showing a peak in 2004/05 after the dry year in 2002/2003. Nevertheless, the increase was much stronger in the N+ group and the groups differed significantly since 2001/02 (Tab. 2.3).

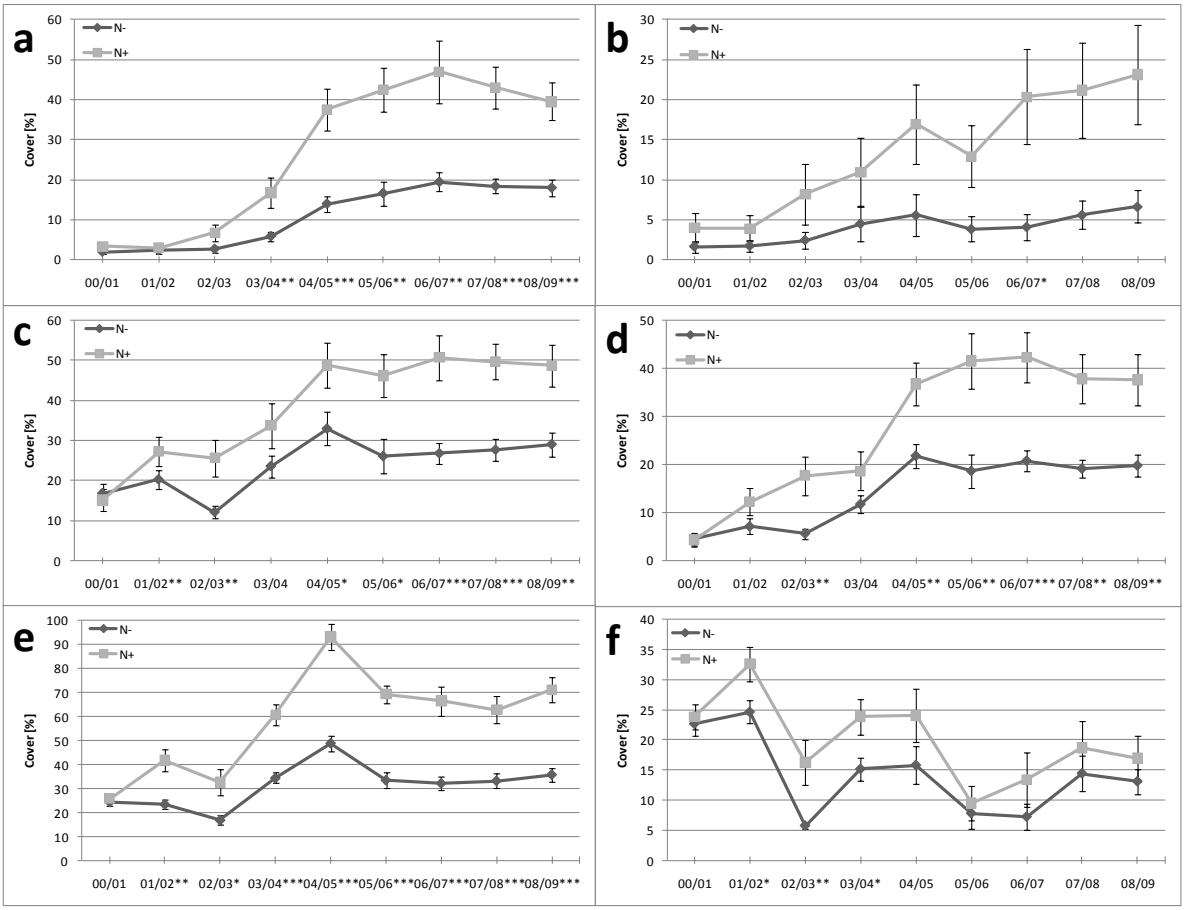

Figure 2.5: Cover of additional parameters and traits after pooling into treatment groups. a. Growth height 3 (> 50 cm); b. Geophytes; c. Hemicryptophytes; d. Strategy type "csr"; e. Seed bank transient; f. Seed bank persistent. Years with significant differences between N– and N+ treatment groups are marked * at the x-axis labels.
Error bars = standard error.

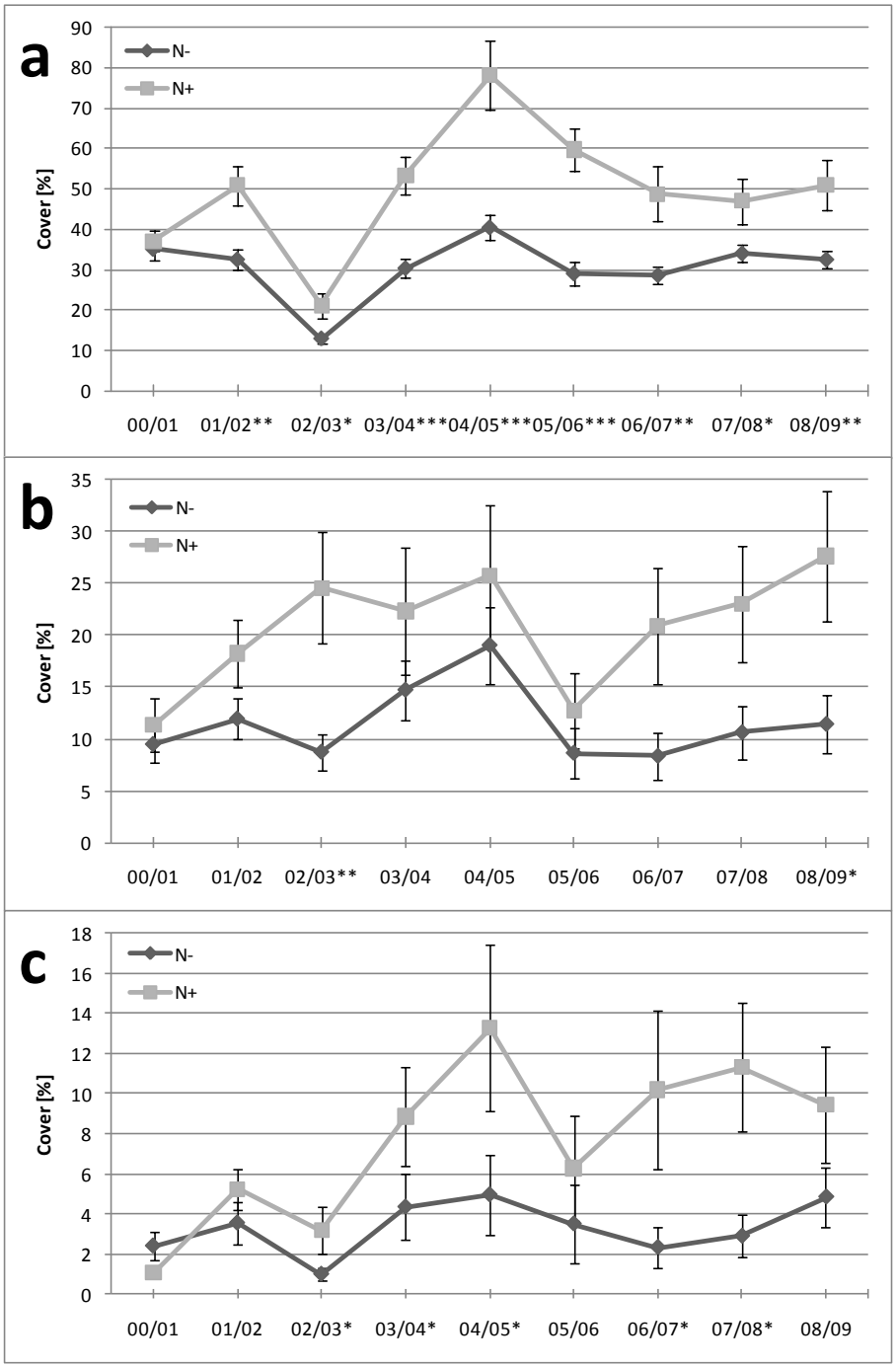

Figure 2.6: Cover of different reproduction types after pooling into treatment groups. a. Reproduction type "s/ssv"; b. Reproduction type "sv", c. Reproduction type "v/vvs". Years with significant differences between N– and N+ treatment groups are marked * at the x-axis labels. Error bars = standard error.

Most plant species in our community show reproduction by seeds only (reproduction type "s"; 67 % of all studied species). Therefore, we added the rather small group "mostly seeds" ("ssv"; 9 %) to this group for the analyses. Likewise, we combined the types "v" and "vvs". As a result, NP, NPK and NPKM treatments affected the cover values of the combined reproduction group ("s/ssv") as shown in Tab. 2.3 significantly. NPK and NPKM treatments differed significantly from the control. Pooling into treatment groups indicates a marked decrease of both treatment

groups in 2002/03 and a recovery afterwards (Fig. 2.6a). This increase in cover values was very strong within the N+ group, from 20 % in 2002/03 up to 80 % in 2004/05 but turned into a decrease since 2005/06 to a level of about 50 %. Cover values of the N– group remained at a level of 30 % after the recovery in 2003/04 (Fig. 2.6a). Treatment groups differed significantly every year of the investigation since 2001/02 (Tab. 2.3). Furthermore, the cover of the treatment groups of the reproduction types "sv" and "v/vvs" differed significantly and showed an increase due to high-dose N (Tab. 2.3; Fig. 2.6b,c).

The qualitative target species ratio (TSR_{qual}) was lower within the N+ group compared to the N– group (Fig. 2.7a). Differences between the treatment groups were significant (Tab. 2.2) and visible since 2004/05, but only the years 2005/06 and 2006/07 differed significantly (Tab. 2.2).

The cover of phanerogams which belong to "Red Data" species increased in 2003/04 in the N+ as well as in the N– group and decreased again in 2005/06 which is depicted in Fig. 2.7b, but the decrease was stronger within the N+ group and cover values remained at a lower level than in the N– group. The n and P treatments increased the cover of "Red Data" species slightly, and treatment groups were significantly different in 2005/06, 2007/08 and 2008/09 (Tab. 2.3).

Ellenberg indicator values (weighted and unweighted) for nitrogen are depicted in Fig. 2.7c and 2.7d. There was no significant effect of single treatments but after pooling of treatment groups (Tab. 2.2), the values were significantly higher in the N+ group in several years.

Only for cover values of *Bromus tectorum* and *Medicago minima* were significant effects of treatments detectable (Tab. 2.3).

In case of *Bromus*, the three high-dose N treatments, NP, NPK and NPKM led to an increase in cover. Values of the N+ group increased 4- to 5-fold between 2003/04 and 2005/06 and differences of both treatment groups were significant in the years 2002/03 to 2005/06 (Fig. 2.8a, Tab. 2.3). As shown in Fig. 2.9a, NPK treatment led to 18-fold higher cover values of *Bromus* in 2004/05 than on control plots. The cover of *Medicago* was significantly higher in the N– group compared to the N+ group in 2007/08 and 2008/09 (Fig. 2.8d; Tab. 2.3). In this case, the P treatment led to a 4.5-fold increase in cover in 2008/09 (Fig. 2.9b). The cover of *Centaurea stoebe* s.l., *Verbascum phlomoides* and *Cetraria aculeata* was significantly affected by the factor treatment group. *Cetraria* showed about 2- to 3-fold higher cover values in the N– group; the other two species had increased cover values in the N+ group (Fig. 2.8b,c,e; Tab. 2.3).

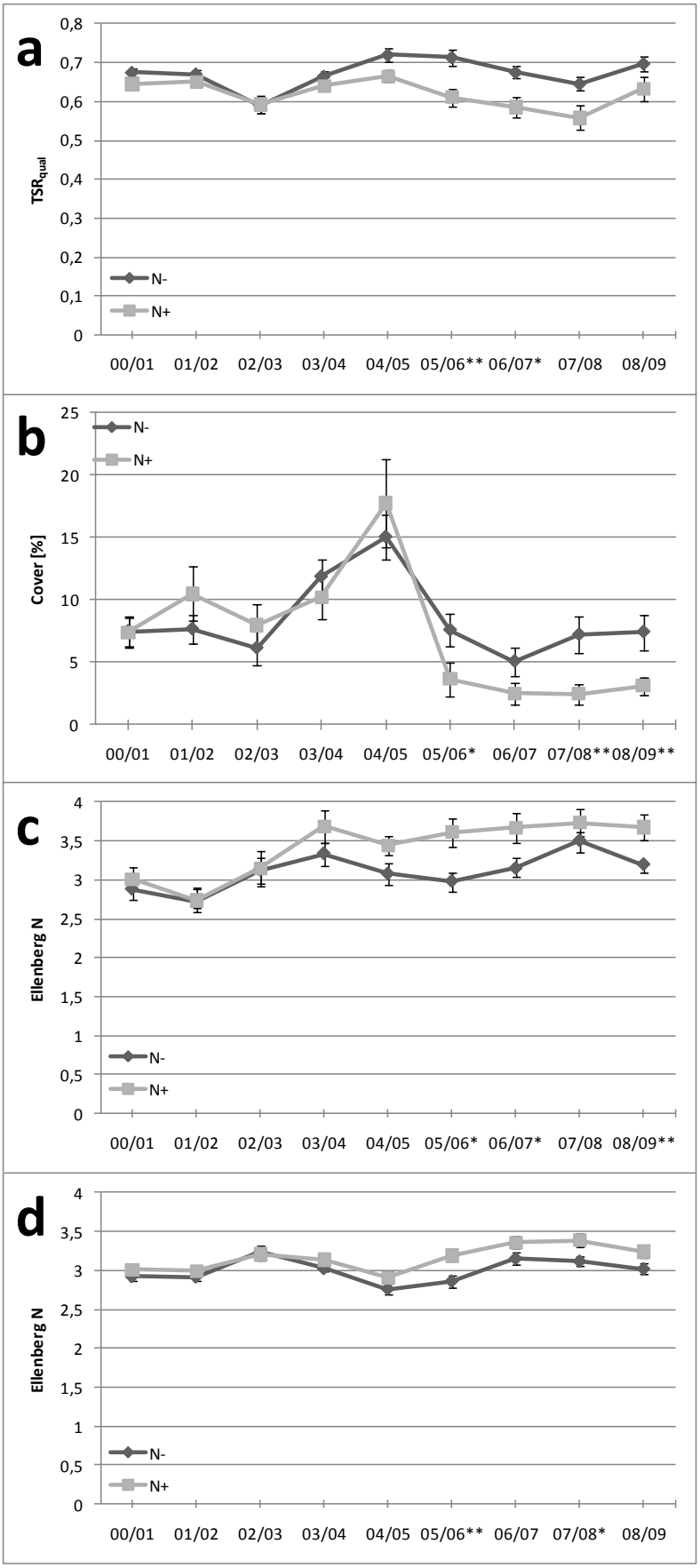

Figure 2.7: Target species ratio (TSR_{qual}, a), cover of "Red Data" phanerogam species (b) and Ellenberg indicator values for nitrogen (c. weighted, d. unweighted) after pooling into treatment groups. Years with significant differences between N– and N+ treatment groups are marked * at the x-axis labels. Error bars = standard error.

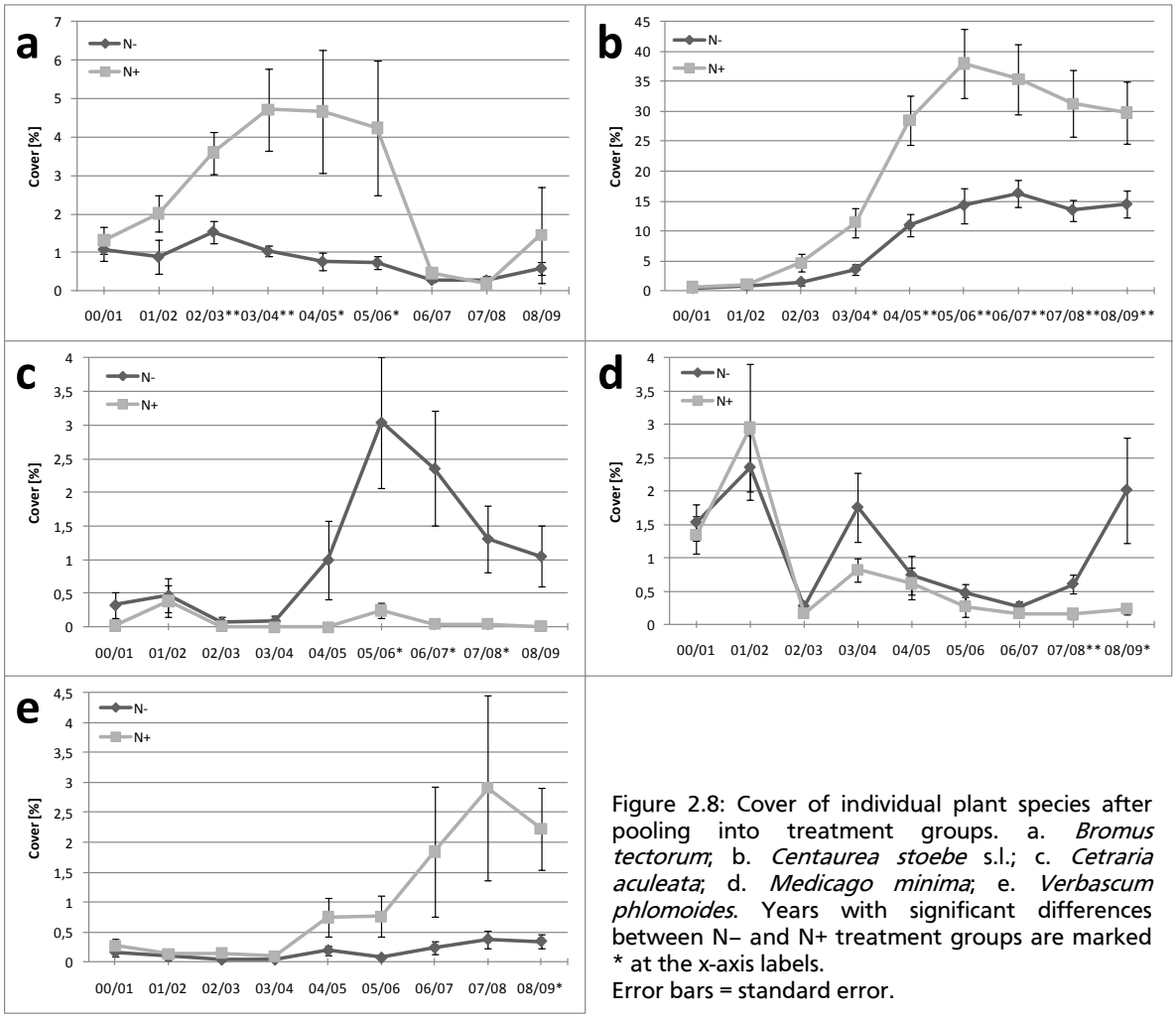

Figure 2.8: Cover of individual plant species after pooling into treatment groups. a. *Bromus tectorum*; b. *Centaurea stoebe* s.l.; c. *Cetraria aculeata*; d. *Medicago minima*; e. *Verbascum phlomoides*. Years with significant differences between N– and N+ treatment groups are marked * at the x-axis labels.
Error bars = standard error.

Phytomass

The phytomass of "legumes" was not significantly affected either by the factor treatment or by the factor year. Therefore, we added them to the phytomass of "graminoids and herbs" (= phytomass of "phanerogams").

All analysed variables show a significant effect of the year (Tab. 2.3). The phytomass of "phanerogams" on control plots was lowest in 2002 (79 g m^{-2}) and highest in 2005 (149 g m^{-2}). Furthermore, the factor treatment significantly affected all dependent variables with except for "roots" and "lichens" (Tab. 2.3). The high-dose N treatments led to a significant increase in case of "phanerogams" and "litter" whereas C, P and n treatment were insignificant compared to the control (Fig. 2.10a,d). With dependence on the year and treatment the increase of "phanerogams" among the N, NP, NPK or NPKM plots was between 2- and 3-fold higher (Fig. 2.10a) and in case of "litter" it was up to 5-fold higher compared to the control set at 100 % for each year (Fig. 2.10d). Besides, the phytomass of "cryptogams" was significantly reduced due to high-dose N but there was a slight increase with C addition, which

was significant in 2004 (Fig. 10b) and caused by the phytomass of “lichens”. If “cryptogams” were separated into “bryophytes” and “lichens” the significant reduction of “bryophytes” was obvious: predominantly plots with NPKM treatment showed a 4-fold lower amount of phytomass (Fig. 2.10c).

After treatment pooling into N–/N+ groups, the factor treatment group was significant for “phanerogams”, “cryptogams”, “litter” and “bryophytes” (and slightly insignificant for “roots”) and post-hoc tests showed significant differences between the two groups concerning nearly all investigated years (Tab. 2.3).

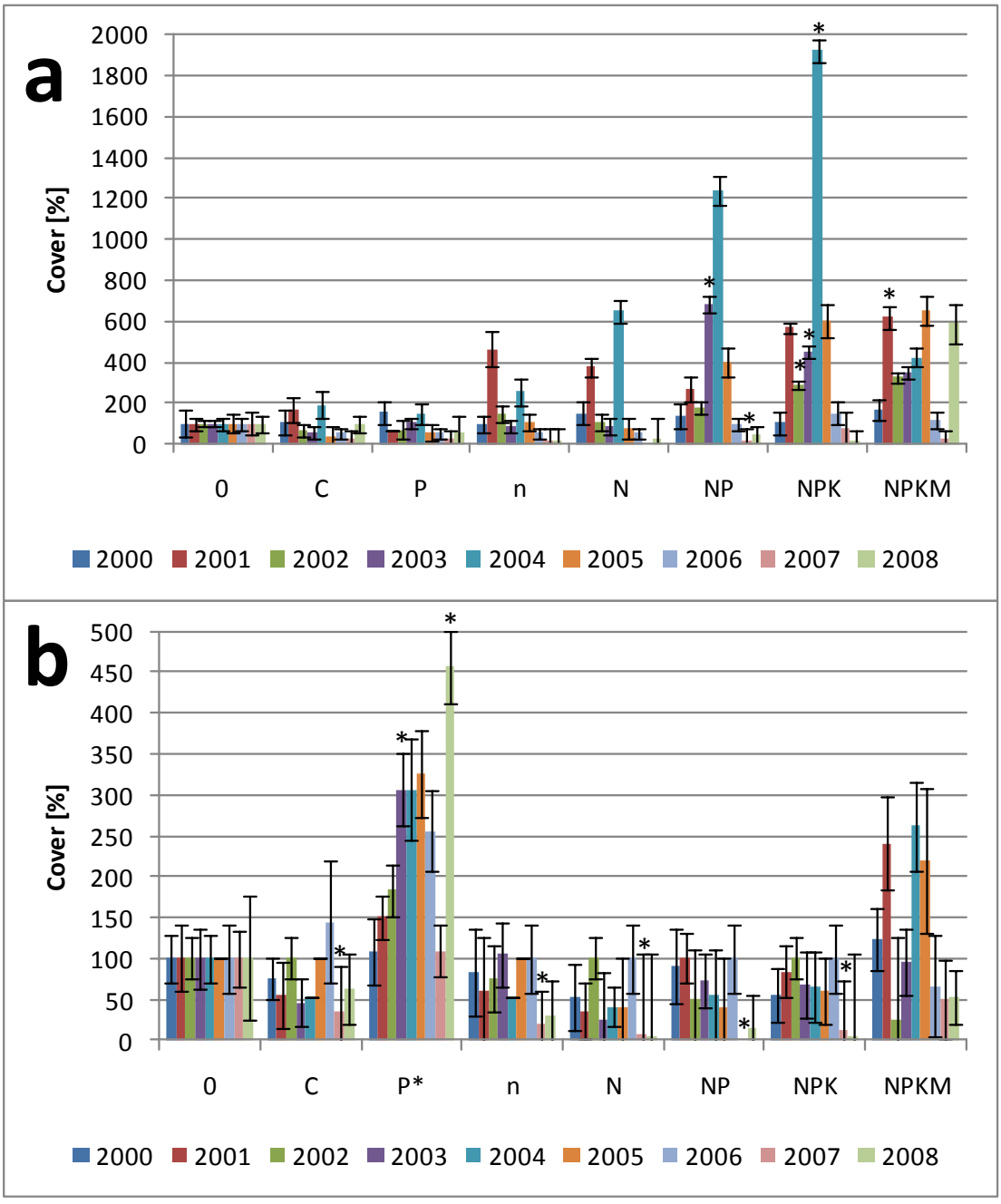

Figure 2.9: Relative cover of *Bromus tectorum* (a) and *Medicago minima* (b). Treatment effects that are significantly different from the control for effect years (2001-2008) are marked * at the x-axis labels and for a certain year over the bar of the year concerned. The cover of the control is set at 100 % for each year.
Error bars = standard error.

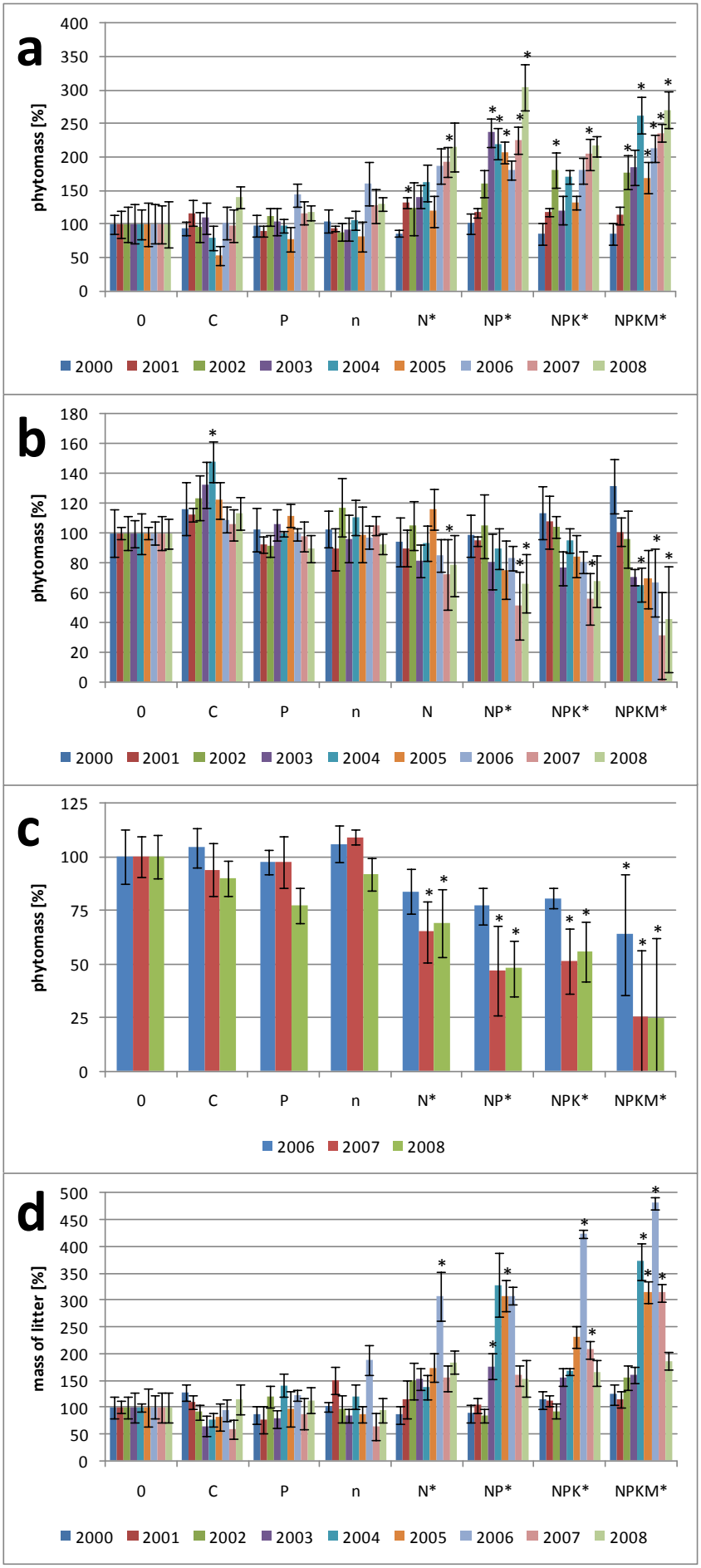

Figure 2.10: Phytomass of different plant functional types and litter. a. Phanerogams; b. Cryptogams; c. Bryophytes; d. Litter. Treatment effects that are significantly different from the control for effect years (2001-2008; bryophytes: 2006-2008) are marked * at the x-axis labels and for a certain year over the bar of the year concerned. The cover of the control is set at 100 % for each year.
Error bars = standard error.

The growth height of all measured individual species was significantly increased by specific treatments with the exception of *Medicago minima* and *Silene otites*, which is shown by a very low N+:N– group ratio (Tab. 2.4). Plants of *M. minima* were significantly smaller in the case of N in high dose, whereas the response of *S. otites* was rather indifferent and only differences between the control and NPKM treatment were significant. Plots with strong N input showed significantly fewer numbers of individuals of *Medicago minima* and *Veronica praecox*. Both species were more abundant on control plots and even with P treatment. In 2006, individuals of *Medicago* were completely missing on N and NPK treatment plots.

Furthermore, treatment led to an increased fecundity (number of capsules or seeds) of all analysed species (Tab. 2.4). Again, pooling into treatment groups showed significant differences between the N+ and N– treatment group concerning nearly all analysed species and additional parameters (Tab. 2.4).

Table 2.4: Extended approach. Results of the mixed linear models of growth height, number of individuals and fecundity of individual species. The first section describes a model for the eight individual treatments, the second section a model for the two treatment groups N+/N– after pooling. Figures <1 in the 'Ratio' column indicate depression by high-dosage N. The ratio was calculated using mean values of the examined years of both treatment groups. Parameters: GH: growth height, I: number of individuals, C: number of capsules, S: number of seeds. A dash indicates that no analysis of this species in the specific year was done. No dash indicates a parameter of a species which was analysed only for a single year. Significant results are shown (in bold print); *p* = level of significance.

	Parameter	Treatment	Year	Treatment *year	Treatment group	Ratio N+:N– group	Treatment group*year4	Treatment group*year5	Treatment group*year6	Treatment group*year7	Treatment group*year8	Treatment group*year9
Species		*p*	*p*	*p*	*p*		*p*	*p*	*p*	*p*	*p*	*p*
Bromus tectorum	GH	**<0.0001**			**<0.0001**	1.8						
Centaurea stoebe s.l.	GH	**<0.0001**	**<0.0001**	0.3017	**<0.0001**	1.3	-	**0.0049**	**0.0025**	**<0.0001**	-	-
Erophila verna	GH	**0.0034**			**<0.0001**	1.1						
Medicago minima	GH	**0.0215**			**0.0004**	0.5						
Medicago minima	I	**0.0038**	**0.0008**	0.2044	**0.0001**	0.3	-	**0.0064**	**0.0003**	-	-	-
Phleum arenarium	GH	**<0.0001**	**<0.0001**	**0.0286**	**<0.0001**	1.3	-	**-**	**0.0002**	**0.0008**	-	0.1966
Saxifraga tridactylites	GH	**<0.0001**	**<0.0001**	0.4917	**<0.0001**	1.3	-	**<0.0001**	**<0.0001**	**<0.0001**	-	-
Saxifraga tridactylites	C	**0.0051**	**<0.0001**	**0.0114**	**<0.0001**	1.5	-	**<0.0001**	0.7619	**<0.0001**	-	-
Saxifraga tridactylites	S	**<0.0001**			**0.0004**	1.2						
Silene conica	GH	**<0.0001**	**<0.0001**	**0.0244**	**<0.0001**	1.3	-	**<0.0001**	**<0.0001**	-	-	-
Silene conica	C	**0.0003**	**<0.0001**	0.4178	**<0.0001**	1.5	**<0.0001**	**<0.0001**	**0.0013**	-	-	-
Silene otites	GH	**0.0222**			0.0617	0.4						
Veronica praecox	GH	0.1842			**0.0484**	1.1						
Veronica praecox	C	**0.0006**			**0.0004**	1.1						
Veronica praecox	I	**<0.0001**	**0.0241**	0.0837	**<0.0001**	0.2	-	-	-	-	**<0.0001**	**0.0002**

We found a total of 2154 seeds belonging to 55 different taxa in the funnel traps during the investigated time frame of about 12 months (Tab. 2.5). Additionally, we recorded 17 small thalli fragments of *Tortula ruraliformis*. The main amount of seeds was trapped between end of October and mid of November in 2009. Our most abundant species were *Conyza canadensis*, *Salix* spec. and *Verbascum phlomoides*. The

ratio of target species among the trapped seeds was quite high (TSR_{qual}: 0.40), but due to the large number of *Conyza* diaspores the TSR_{quant} was low (0.20). The percentage of trapped seeds of species actually present in the vegetation of our plots ("autochthonous seeds") was very high (82 %). The TSR_{qual} of these seeds was 0.65, which corresponds quite well with the TSR_{qual} of the present vegetation (about 0.70 in 2008/09, Fig. 2.2). The TSR_{quant} of the autochthonous seeds was lower (0.24). Of the "allochthonous seeds" most seeds belonged to non-target species (TSR_{qual}: 0.12, TSR_{quant}: 0.03). For example, all seeds of tree species like *Betula pendula* and *Salix* were found in this group (Tab. 2.5). In addition, we found two caryopses of *Calamagrostis epigejos* in two traps from two different blocks in which *Calamagrostis* was actually not present.

Table 2.5: Results of the catches in seed funnel traps in the five experimental blocks between November 2008 and December 2009. SG: species group (t: target species, n: non-target species, w: woody species). F: frequency of catch events in the five experimental blocks. Catches of single traps within one block were pooled.

SG	**a) Found in trap(s), present on plots in the respective block**	No. of seeds	F	SG	**b) Found in trap(s), not present on plots in the respective block**	No. of seeds	F
n	*Conyza canadensis*	1042	5	w	*Salix* spec.	289	5
n	*Verbascum phlomoides*	255	4	n	*Solanum nigrum*	25	3
t	*Silene otites*	78	4	w	*Betula pendula*	25	5
t	*Cerastium semidecandrum*	67	4	w	*Sambucus nigra*	9	4
t	*Silene conica*	64	5	t	*Potentilla* cf. *recta*	8	1
n	*Geranium molle*	43	4	w	*Acer negundo*	4	2
t	*Arenaria serpyllifolia* agg.	38	4	n	*Sisymbrium altissimum*	3	2
t	*Helichrysum arenarium*	33	5	w	*Pinus sylvestris*	3	2
t	*Centaurea stoebe* s.l.	29	5	w	*Populus* spec.	3	3
t	*Euphorbia cyparissias*	18	4	n	*Calamagrostis epigejos*	2	2
t	*Vicia lathyroides*	18	5	n	*Viola tricolor* agg.	2	1
t	*Rumex acetosella* s.l.	15	3	t	*Acinos arvensis*	1	1
t	*Myosotis stricta*	12	2	n	*Cirsium arvense*	1	1
t	*Petrorhagia prolifera*	8	3	n	*Corispermum leptopterum*	1	1
t	*Koeleria macrantha*	6	1	n	*Daucus carota*	1	1
n	*Poa angustifolia*	6	2	n	*Epilobium tetragonum*	1	1
n	*Bromus tectorum*	5	3	t	*Herniaria glabra*	1	1
t	*Phleum phleoides*	4	1	n	*Rumex thyrsiflorus*	1	1
t	*Phleum arenarium*	3	1	n	*Senecio vulgaris*	1	1
t	*Ononis repens*	3	1	n	*Taraxacum* spec.	1	1
t	*Saxifraga tridactylites*	3	2	n	*Vicia* cf. *villosa*	1	1
n	*Setaria viridis*	2	2	n	*Rubus spec.*	1	1
n	*Crepis capillaris*	2	1	w	*Acer pseudoplatanus*	1	1
n	*Senecio vernalis*	2	1	w	*Ailanthus altissima*	1	1
n	*Carex hirta*	1	1	w	*Prunus serotina*	1	1
t	*Poa bulbosa*	1	1		Brassicaceae	1	1
t	*Erodium cicutarium* agg.	1	1		Orchidaceae	2	2
t	*Medicago minima*	1	1				
n	*Salsola kali*	1	1				
n	*Veronica arvensis*	1	1				
t	*Tortula ruraliformis* (thalli fragments)	17	5				
	Indet.	2	1				
	Total no. of a) - autochthonous seeds	1781			Total no. of b) - allochthonous seeds	390	
	TSR_{qual}	0.65			TSR_{qual}	0.12	
	TSR_{quant}	0.24			TSR_{quant}	0.03	

Discussion

Direction and speed of succession

One proposed mechanism of succession is described by the facilitation model. This theory suggests that an unoccupied habitat is initially exploited by pioneer species that are capable of establishing themselves. These species modify the site and make it more suitable for the following species by, e.g. initiating a further soil development. The impact of biotic interactions can influence all stages of succession (Walker & Chapin III 1987) and each life history stage of the dominant species (Walker et al. 2003). Consequently, the pioneer species of the initial stages, which are predominantly small or short-lived or species from other ecological strategy types, are displaced or replaced by mid- or later-successional species through competition. This is conistent with studies by Tilman (1987) or Huberty et al. (1998), and these findings can be caused by light competition (Olff et al. 1993), proceeding soil development or lack of gaps. Additionally, litter accumulation can negatively affect species richness or the regeneration and survival of plants, e.g. of annuals (Sydes & Grime 1981a,b; Süss et al. 2004; Weltzin et al. 2005). Thus, the change in plant species dominance over time is caused by modifications in the abiotic environment that are imposed by the developing community.

In base-rich inland sand ecosystems the typical successional pathway leads from pioneer stages of Koelerio-Corynephoretea vegetation to species-rich stands of Allio-Stipetum vegetation (Süss et al. 2010). Succession can also be influenced by the community's response to disturbance, species life histories, species interactions, plant establishment, competition and nutrient dynamics (Walker & del Moral 2008). Recently, results from permanent-plot studies have pointed out the stability of open sand vegetation on nutrient-poor soils for over ten years (Süss et al. 2010). Additions of fertilisers are known to trigger new shifts in trajectories (Walker & del Moral 2008). Hence, the course of succession of our ecosystem type can come along with the development of non-typical species-poor vegetation stages especially when habitats show increased P-values (Süss et al. 2004). A co-limitation of nitrogen and phosphorus in calcareous sandy soils can occur due to the low solubility of calcium phosphate (Kooijman et al. 1998).

We revealed two main successional pathways: one which reflects the supposed "typical" line, and another one which is clearly separated. For most analysed parameters the separation into these two pathways became distinct only after a five-year period of nutrient addition. It is assumed that there is probably a "lag phase" which is needed before the community structure responds to changed nutrient conditions. These findings again emphasise the importance of long-term observations for the study of vegetation dynamics (Bakker et al. 1996; Schmidt et al. 2009). As

shown by the DCA diagram, both treatment groups were more or less strictly separated from each other, but, nevertheless, plots with solely N treatment were more intermediate between N– and N+ treatment groups than plots with N and P in combination or plots with NP and additional K. Nutrient addition led also to an accelerated rate of succession because plots with N + P addition moved approximately 1.5-fold further on axis 1 than the other plots. Especially the balance between N and P levels in both soils and plants can affect successional processes (Sterner & Elser 2002).

The local airborne nitrogen deposition was low and there were only slight negative effects of a moderately increased atmospheric nitrogen deposition (additions of low dose N) for one parameter (lower species number of "r" strategists), which can be neglected because these effects were only visible for two years (2006/07 and 2007/08) but not for the following. Hence, we can exclude that an enhanced airborne nitrogen deposition can cause an increase in vegetation density, grass dominance or a loss of species diversity within a time frame of eight years, which is in line with Wilson et al. (1995). Nevertheless, Stevens et al. (2004) concluded that long-term chronic N depositions have significantly reduced plant species richness and that especially species adapted to infertile conditions are systematically reduced at high N depositions.

The addition of a carbon source like saccharose, sawdust or mulch to induce an immobilisation of plant-available nitrogen due to an increase of microbial N uptake was often discussed as a useful tool for restoring N-limited plant communities and, hence, as restoration measure (see Török et al. 2000; Blumenthal et al. 2003). Other authors, however, found no evidence for a successful restoration of native species by adding carbon, or significant effects on the vegetation, respectively (Morecroft et al. 1994; Corbin & D'Antonio 2004). The DCA diagram has revealed a slightly separated position of plots with C addition more or less very oppositional to all high-dose N plots, indicating a course of succession contrary to the N+ treatment plots. Furthermore, the phytomass of cryptogams (especially lichens) slightly increased with C addition. This may be related to the small amount of competitive species on these plots. Anyhow, nitrogen is not always the limiting resource for plant growth. If plant growth is limited by water, changes in N availability might have little effect on grassland invasions by weeds, because experiments by Blumenthal (2009) have shown that C addition was helpful against invasive species only in plots with a sufficient water supply. However, the experiment by Alpert & Maron (2000) shows that C addition can help to counteract the invasion of grasslands by non-native plants, when the invasion is N-promoted and the major invasive species are grasses.

The altered course of succession due to nutrient enrichment was as expected and came along with an enhanced accumulation of litter and a decrease of cryptogams. Bryophytes (especially *Tortula ruraliformis*) diminished during succession as reported by Storm & Süss (2008) in initial sand ecosystems, or in acidic dry grassland by Hasse & Daniëls (2006). The reaction among lichens was different: some species profited from nutrient addition, some were suppressed and others first increased and later decreased severely on plots with high dose N, but not on the other ones. Above-ground phytomass production of phanerogams was more than doubled by the N, NP, NPK and NPKM treatments, which is consistent with Willems et al. (1993) and Gough et al. (2000), and is therefore again evidence for nutrient limitation. A pronounced P-limitation was visible among most legumes and is in accordance with Bobbink (1991) or Mamolos et al. (1995). As an example, *Medicago minima* profited on one hand significantly by P treatment but on the other hand it was reduced by N treatments. However, *Medicago* and other legumes profited by NPKM treatment showing a limitation by macronutrients as well as a co-limitation by micronutrients.

Nutrient addition can increase the number of local plant extinctions, the species composition and composition of functional groups can rapidly change (Lanta et al. 2009). But this is not consistent with our findings because we found no changes detectable in the first five years ("lag phase"). Prach & Pyšek (1999) specify the "ideal successional dominant" with the following characteristics: tall, wind-pollinated, a geophyte capable of lateral spread, preferring high nutrient supply. The species which increase during succession have better means of long-distance dispersal and are often more competitive (Römermann et al. 2008). Particularly ruderal species have the ability to spread laterally in common (Prach & Pyšek 1999) and establish during an advanced succession (Kahmen & Poschlod 2004; Poschlod et al. 2009). Our results correspond with these findings. The cover of competitive graminoids was between 3- and 4-fold higher in the N+ group compared to the N– group in the years 2006/07 to 2008/09 and, besides, non-competitive graminoids strongly decreased at the same time.

We could demonstrate the facilitation of geophytes, hemicryptophytes, tall species, "csr" strategists and reproduction types ("s/ssv", "sv", "v/vvs") by nutrient application. The latter three parameters characterise, for instance *Centaurea stoebe* s.l., which is known to be strongly N-limited (Storm & Süss 2008), and it was also the decisive species among the reproduction type "s/ssv". The group of geophytes consisted mainly of graminoids like *Carex hirta*, *C. praecox* and *Elymus repens*, which are on the other hand successful competitors. Both *Carex* species and herbs like *Asparagus officinalis*, *Helichrysum arenarium* or *Rumex acetosella* caused the main cover abundances among the "sv" type, whereas mainly the grasses *Calamagrostis*

epigejos, *Cynodon dactylon*, *Elymus repens* and *Poa angustifolia* created the "v/vvs" reproduction type and were facilitated by nutrients. Süss et al. (2004) pointed out that grass encroachment can be expected for mid-successional grassland stages in our area.

Furthermore, the extended approach has shown that nearly all analysed species were facilitated by N and P additions, whereas legumes profited by N addition only in combination with macro- and micronutrients. This indicates the co-limitation of the main element N by P, which is in agreement with different authors (e.g. for calcareous grasslands: Bobbink 1991; Morecroft et al. 1994; Kooijman et al. 1998; Janssens et al. 1998; for dry grasslands: Mamolos et al. 2005; Storm & Süss 2008).

Effects on phytodiversity and threatened species

Phytodiversity was stable in the first two years of the study but diminished on all plots in 2003 as a consequence of the extreme weather conditions in this extraordinary year. There are other data sets for our area showing the same effects (e.g. Faust et al. 2011). This abiotic stress affected many species but predominantly annuals and therefore species from the ecological strategy types "s/sr" and "r" (sensu Grime 1979). There was a slight recovery on all plots in the following years of the study. Year-to-year fluctuations of abiotic variables like moisture are responsible for year-to-year fluctuations in frequency of occurrence of many short-lived species (Olff et al. 1993). These findings can explain the significant influence of the main effect "year" throughout all investigated variables and also that precipitation strongly impacts the development of the vegetation, which is consistent with experiments by Süss et al. (2007) at the same site. Thus, water seems to be another limiting factor for our ecosystem. However, plots with high dose nitrogen showed a decrease in species numbers after the lag phase of about five years. As a result, phytodiversity was about five species lower than on plots without nitrogen in higher doses.

Huberty et al. (1998) pointed out that the community response to N addition primarily is expressed through changes in community structure, not richness, and our findings revealed important changes after the continuation of the former experiment by Storm & Süss (2008). Changes in abundance of single species express considerable dynamics within the vegetation, whereas the species' response depends on one hand on extreme weather conditions and the successional phase of the grassland and on the other hand on the competition situation (Hasse & Daniëls 2006). Süss et al. (2007) detected a negative relationship between plant species richness and productivity for early and mid-successional stages of nutrient-poor sand grasslands. So, sandy pioneer grasslands with a high species diversity can alter into vegetation with only a few competitive species after fertilisation. We detected that the species number as well as the cover of threatened (according to "Red Data")

species diminished. They are target species and belong to early successional stages of our community. Such changes are known from several studies (e.g., Schellberg et al. 1999; Shaver et al. 2001; Carroll et al. 2003; Jacquemyn et al. 2003). A shift in species composition can even be induced by P, as is known from fen meadows on nutrient-poor soils (van der Hoeck et al. 2004). Additionally, Hejcman et al. (2007) pointed out that species of low-productive grasslands survived in plots with N only but not in combination with P or K. Thus, N enrichment can be detrimental to species richness but only if accompanied by another limiting nutrient like P, which was shown by our experiment.

Seed availability

Pioneer communities are often highly heterogeneous and determined by dispersal availabilities (Lepš et al. 2000). The soil seed bank can adversely affect typical trajectories of a community due to a hidden pool of colonists and should be considered carefully (Satterthwaite 2007). Earlier studies from our experimental site or similar sites concerning soil seed bank analyses (Stroh et al. 2002; Eichberg et al. 2006) have shown that most species found were already present in the above-ground vegetation. Nutrient addition facilitated species with a transient seed bank type but not the seed bank of those species which had a persistent one. Again, this was caused by species like *Centaurea* or graminoid species, which were dominant among the transient type. Experiments in which different seed mixtures are sown over existing vegetation have shown that natural colonising species were suppressed, and the whole successional pathway was affected by sowing plants due to markedly altered successional trajectories (Lepš et al. 2007). Neighbourhood effects (e.g. the local seed rain or species pool) can affect the earlier phase of succession (Baasch et al. 2009). The seed rain in our study consisted partly of autochthonous seeds but, nevertheless, nearly one-fifth of the seeds in the traps were allochthonous, among them mainly non-target species like various trees or ruderal herbs. The high amount of *Solanum nigrum* seeds was probably caused by contamination via bird faeces. Even fruits of *Calamagrostis epigejos* were found in traps within experimental blocks where this species was not currently present. This dominant grass is well known for its clonal strategy; there are probably only rare dispersal events. Hence, seed availability is an important limitation of plant species abundance and distribution (Ehrlén et al. 2006), and dispersal limitation can be one factor controlling the rate of early secondary succession (Lepš et al. 2007).

It could be shown by this experiment that the floristic structure, successional lines, phytodiversity and plant strategies of the studied system were changed after a five-year period and a threatened vegetation type was gradually replaced by one with dominant and/or competitive species. These findings emphasise the importance of long-term observations for the study of effects caused by nutrients.

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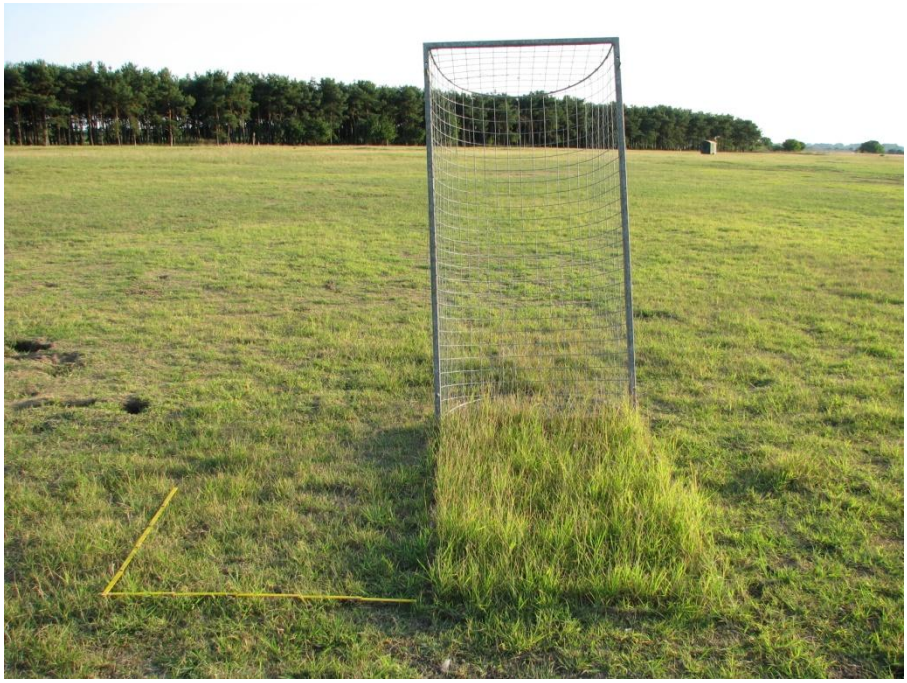
Threatened inland sand vegetation in the temperate zone under different types of abiotic and biotic disturbances during a ten-year period

Exclosure (split-plot) in July 2006 showing the high grazing pressure and flower reduction at the study site. Foreground: with rabbit grazing; background: without grazing.



Mini-exclosures (right) and adjacent comparative plots (left)
were used to investigate the phytomass production and extraction by rabbits.

Abstract

In sandy grassland vegetation of Central Europe, extensive grazing is often a management tool to maintain and improve nature conservation value. As part of a long-term field experiment lasting 10 years we investigated the beneficial effects of sheep grazing as a type of moderate disturbance. As “experiments by nature” happened in this time period we were also able to study severe biotic (rabbit grazing) and abiotic (drought) disturbances, examining the recovery and resilience of the system after these severe disturbances.

Within a six-fold replicated randomised split-plot design, 25-m² plots of Armerio-Festucetum trachyphyllae vegetation were studied from 2000-2009 in the northern upper Rhine valley (Germany). We analysed sheep-grazed and non-grazed plots (both with very low rabbit impact until 2005). In 2005 we established an additional plot type without rabbit and sheep grazing. Severe rabbit impact was studied in detail from 2006 to 2008 concerning flower resources, seed production, endozoochorous seed dispersal and phytomass extraction. Data were analysed by ordination methods and mixed linear models.

Moderate disturbance by sheep grazing maintained species diversity in times of low rabbit densities. Severe drought in 2003 resulted in a marked decrease of species numbers, but the system recovered already in 2004. The subsequently analysed “high rabbit impact” resulted in decreases of species numbers, cover of bryophytes, flower and seed quantities and seed content in faeces. Species numbers also declined on plots without grazing, but for different reasons, e.g. the increase of litter. Flower phenology was not affected. After the decline of the rabbit population, species numbers slightly increased in 2009. Non-grazed plots showed a decrease of bareground and increase of litter.

Despite severe disturbances by rabbits or drought, the community structure was relatively stable and showed only slight changes, especially in case of non-ruderalised plots. We developed a conceptual model, showing the high potential of recovery and resilience even in the case of severe disturbances.

Introduction

Threatened sand grassland vegetation is known to be disturbance-driven (Eichberg et al. 2007). Biotic responses to different disturbance types are key factors for the understanding of ecosystem dynamics and therefore relevant for management practices (Malanson & Trabaud 1987; Chapin III et al. 1996; Mitchell et al. 2000). In the Central European cultural landscape abandonment of grazing or cutting often leads to loss of phytodiversity (Dupré & Diekmann 2001) and to grass encroachment (Kooijman & van der Meulen 1996). To ensure disturbance dynamics, extensive livestock grazing seems to be an important management tool causing intermediate-disturbance effects and the creation of gaps (e.g., Süss et al. 2004, Eichberg et al. 2007). Microsites thus generated may facilitate the germination of plant individuals (Bakker 2003; Blomqvist et al. 2006; Donath et al. 2007) and are necessary in sandy grasslands for a successful establishment of plants (Süss & Schwabe 2007; Eichberg et al. 2007).

Beside the expected beneficial effects of grazing disturbance for the system, there are periodically or episodically severe disturbances, which are hardly predictable. On one hand these are extreme weather conditions like dry summers (which probably will increase in the course of global change, see EEA 2004), and on the other hand extreme biotic factors. An example of such biotic factors, which cause severe disturbances, is the impact of large rabbit populations. Moderate rabbit impacts mostly cause an increase of plant species richness (e.g., Zeevalking & Fresco 1977; Bakker 2003; Bakker & Olff 2003; Delibes-Mateos et al. 2007).

Primarily our task was to study effects of grazing disturbance (in our case sheep grazing) to sample basis data for the conservation management of our system (Armerio-Festucetum trachyphyllae sandy grassland). As yet there are only a few data concerning grazing impact on this community type (Süss & Schwabe 2007). We established a one-factorial field experiment (sheep grazing −, +) before grazing started (status quo) late in the year 2000. The pre-grazing state was characterised by extensive mowing and mulching regime each year.

During the ten-year period of the experiment an extremely hot and dry summer occurred (in the year 2003) and afterwards the rabbit population increased with a peak level between 2006 and 2008. To study these rabbit effects, we enlarged our approach in the year 2005 in a phase of still relatively low rabbit population level, by establishing sheep- and rabbit-free exclosures. We additionally ran an extended approach to study effects of high rabbit impact on flower- , fruit-set and aboveground phytomass production.

The two “natural disturbance experiments” (Bruelheide & Luginbühl 2009) enabled us to study severe effects by drought and rabbits. We can distinguish five periods with different disturbance regimes: in Period 1 there was extensive mulching and mowing before our experiment started. Period 2 was characterised by a moderate disturbance by extensive sheep grazing, while Period 3 represents severe

abiotic disturbance (drought). Severe biotic disturbance by rabbit grazing is characteristic for period 4, and period 5 is influenced by the decline of the rabbit population. Especially the resilience of our system and recovery after strong disturbances are central questions of our study. Our aim is develop a conceptual model for the system's response to these disturbance regimes. Generally, it depends on the disturbance characteristics like magnitude or time (Glenn-Lewin & van der Maarel 1992) whether the vegetations' response is resistance, recovery or resilience or whether the changes are irreversible (Connell & Slatyer 1977; van de Koppel & Rietkerk 2000).

Leading hypothesis during the long-term study were (1) that moderate disturbance by sheep grazing will be beneficial for the maintenance of our system and (2) that there will be a recovery after severe abiotic one-year disturbance, but (3) we doubt that recovery will be successful after several years of strong biotic stress (rabbit over-grazing). In this way, patterns and mechanisms of eventual successional processes should be characterised.

Therefore, we ask the following questions:

How does the system respond to

- moderate disturbance by extensive sheep grazing, especially in the rabbit-poor period?
- severe abiotic disturbance (drought)? Are there irreversible changes or is there a recovery?
- severe biotic disturbance (intensive rabbit grazing) including flower-, fruit-production and phytomass extraction?
- lack of biotic disturbance in the plots with sheep- and rabbit exclusion in the period of high rabbit population density. Are there successional processes?

Materials and methods

Study site and grazing pressure

The study area, a nature reserve, is located in the northern upper Rhine valley in southwestern Germany (Hesse) ca. 30 km south of Frankfurt/Main near Darmstadt (8°35'E/49°51'N) and belongs to a Fauna-Flora-Habitat area as defined by the EU-Habitats Directive ("Ehemaliger August-Euler-Flugplatz von Darmstadt", 71 ha in general, study site: 6 ha). Mean annual temperature (± SD) in the investigated timeframe is 11.1 ± 0.3 °C in combination with a mean annual precipitation rate of 629 ± 126 mm yr^{-1} (in 2003: 379 mm; Fig. 3.1). Precipitation was high between October 2002 and January 2003 (80.3 ± 13.7 mm; mean precipitation in this timeframe: 46.8 ± 21.7 mm) and very low between February and April 2003 (11.3 ± 2.1 mm; mean precipitation in this timeframe: 45.1 ± 28.6 mm). Additionally, temperature in February 2003 was extremely low (0.4 °C; mean temperature in

February: 3.6 ± 2.1 °C). The annual duration of sunshine is 1701 ± 180 h (in 2003: 2138; data from Frankfurt airport, 2000-2009, Deutscher Wetterdienst).

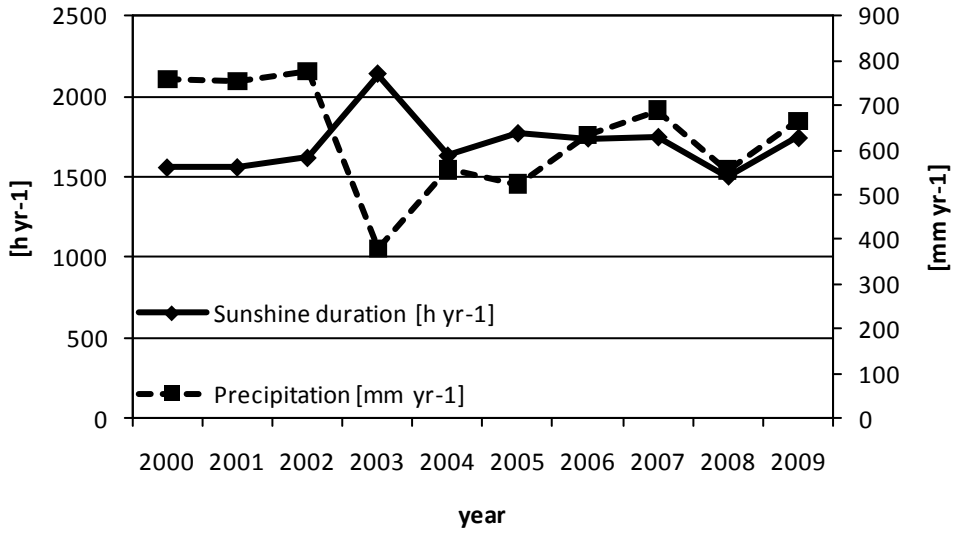


Figure 3.1: Duration of sunshine [h yr-1] and amount of precipitation [mm yr-1] during the investigated time period.

The characteristic plant community of our field experiment belongs to the highly threatened types in Central Europe according to the EU Habitats directive. It can be classified as Armerio-Festucetum trachyphyllae Hohenester 1960, see also Faust et al. (2007). The community forms a middle-successional stage and is threatened by encroachment of grasses such as *Poa angustifolia* and *Cynodon dactylon*. The substrates are primarily calcareous sands which were blown-out during the late glacial and early postglacial period from Rhine deposits. Consolidated stands of the Armerio-Festucetum trachyphyllae show a slight acidification of the topsoil (pH ranges in 0.01 mol l^{-1} $CaCl_2$ from 5.4 to 7.5, $CaCO_3$ content from 0 % to 5.4 %; soil samples (n = 30) were taken in May 2009 at our site). The pre-grazing disturbance state in our system was characterised by a mowing regime during the military use until 1992 and afterwards only by very extensive mowing and mulching.

Sheep grazing by traditional races (Rhoen sheep, Skudde) was newly established in the area in the year 2000. The sheep flock (ca. 170 animals) grazed in the years 2000 and 2001 during summer (mainly from June to August) in paddocks of about 3-4 ha for 10-14 days, sometimes a few days longer. From 2002 on, up to 500 sheep grazed in small paddocks, ca. 1 ha, for 1-9 days. In both cases sheep grazed as long as an adequate food supply could be guaranteed. Population densities of rabbits were estimated once a year by the Hessian Department of Forestry. For the 71-ha area the population size developed in the following way: 2000-2002 between 50 and 150 animals, 2003-2004 between 500 and 750 animals, 2005 between 1000 and 1250 animals, 2006-2008 between 1000 and 2000 animals. In 2009 the rabbit population was estimated as 600-700 animals. The rabbits' grazing impact can be almost neglected in the first three years because of low population densities mainly caused

by the rabbit haemorrhagic disease (RHD) or myxomatosis. Generally, the main rabbit population of the whole nature reserve is concentrated in the studied Armerio-Festucetum part.

Experimental design

The field experiment in the Armerio-Festucetum area started in 2000. The area was stratified into vegetation types and represents the amplitude of this community from typical stands to more ruderalised stands. Six exclosures were randomly distributed, each measuring 14 m x 14 m and fenced against sheep grazing. Rabbits were regarded as a natural factor of the system and the few individuals were able to graze in- and outside the fences. In 2005 all exclosures with sheep exclusion were divided (split-plot design). One half was protected against rabbits with fine chicken-wire netting, which in addition to its above-ground extent was dug 1 m into the soil. Therefore, there is a long-term dataset from 2000 to 2009 with sheep and (first low, later higher) rabbit impact (SR) and with (first low, later higher) rabbit impact and sheep exclusion (R). From 2005 to 2009, additionally six ungrazed plots (N) were studied (2005: status quo): "Extended approach". Each plot (relevé) was 25 m² in size.

The exclosure system is supplemented by a grid point system, which was recorded for the first time in 2000 and lastly in 2007. In total there are 100 unfenced grid plots (GP), each with a radius of 5 m (= 79 m² relevé size, distance between two plots 65 m). Seven of them are adjacent to the exclosures and are included in the analysis of some data. Additionally, to reveal information about species numbers during the former mowing and mulching regime as well as the change to a sheep-grazing regime, we added data from 1999 and 2000 from older permanent plots (n = 4; each relevé 25 m²). These relevés represent relatively consolidated stages of the Armerio-Festucetum (e.g., cover values of *Koeleria macrantha* up to 75 %); therefore species numbers are lower, but the floristic structure corresponds to our plots.

Investigated variables

To detect changes in the floristic structure the vegetation was annually recorded in early summer (May or June), using cover estimates (<1/1/2/3/…/8/9/10/15/20/…/95/100 %). Additionally, analyses of cover abundances were conducted with single plant species. In total 29 species were tested, which reached a degree of presence of over 40 %.

Some analyses took place by the set-up of the Plant Functional Types (PFTs): "graminoids", "legumes" and "other herbs" (without legumes) and, additionally, annuals and perennials. The turnover ratio, which is defined as the quantity (%) of plant species which was exchanged between two recording years, was calculated. A second turnover ratio regarding the reference year 2000 was calculated to get

information about the similarity of the sampling years and the reference year. In addition, we divided all plant species into three different growth heights (GH1 = 0-20 cm; GH2 = 21-50 cm; GH3 > 50 cm), based upon observations in the field. We used the target species ratio (TSR; according to Eichberg et al. 2010) to elucidate whether target species are facilitated due to disturbance or not. Target species are considered as species from the classes Festuco-Brometea (FB) and Koelerio-Corynephoretea (KC). The TSR can be calculated by the following formulas:

TSR_{qual} = (Species number of FB + KC)/Total species number

TSR_{quant} = (Cover sum of FB + KC)/Cover sum of all species

All analyses were carried out qualitatively (species number) as well as quantitatively (species cover).

Nomenclature follows Wisskirchen & Haeupler (1998) for vascular plants, Koperski et al. (2000) for bryophytes, Scholz (2000) for lichens and Oberdorfer (2001) for plant communities. Red Data species were classified according to Korneck et al. (1996).

Extended approach: rabbit impact

In the three years of the extended approach (2006-2008) flower phenology, seed production, potential seed availability in rabbit dung samples and above-ground phytomass production were studied.

Flower phenological records were obtained from spring (April/May) to late summer (September) on the plots with rabbits (R) as well as on the plots without rabbits (N) every week (Faust et al. 2007). A preliminary study showed that flower numbers in 2005 were very similar on both plot types and showed no differences. The phenologically recorded area on each plot was limited to the peripheral zone of the permanent plots, 16 m^2 in size, in order to avoid disturbance effects during the recordings. In 2008 phenological recordings on the complete plot sizes took place and were compared with data from the reduced-size plots to validate them. No important differences were observed. We examined every plant species with a higher degree of presence (species had to be present in at least three R plots and three N plots). In total we analysed 21 single plant species; nine of which are important flower resources for wild bees (Beil et al. 2008; Kratochwil et al. 2009). The method of counting corresponds to the method used by Kratochwil et al. (2002) and was carried out quantitatively using flower phenological units (Table 3.1).

An impact of rabbits on seed production was studied by randomly collecting at least 10 ripe fruits of eight selected herbs (including two Fabaceae species) on R plots as well as on N plots in 2007. We sampled predominantly species which were common at our site. The fruits were opened and the seeds enumerated. By extrapolation with data from the flower phenology recordings of the same year we were able to calculate seed production and its reduction by rabbits.

Studied species	flower units
Armeria maritima ssp. *elongata**	i
*Berteroa incana**	i
*Carduus nutans**	b
Carex hirta	b
Centaurea stoebe s.l.*	b
Cerastium arvense	e
Erodium cicutarium agg.*	e
*Euphorbia cyparissias**	b
*Geranium molle**	e
Medicago falcata (incl. *M.* x *varia*)*	i
Medicago minima	i
Myosotis ramosissima	i
Myosotis stricta	i
Plantago lanceolata	i
Potentilla argentea agg.*	e
Rumex acetosella s.l.	b
Sedum acre	i
Silene latifolia ssp. alba	i
Trifolium campestre	i
Verbascum phlomoides	b
Vicia lathyroides	e

Table 3.1: Phenologically analysed plant species and counted flower units (extended approach): b = flowering individuals, sprouts, e = single flowers, i = inflorescences. * = important entomophilous plant species for wild bees (Beil et al. 2008).

To test the potential seed availability of rabbit dung samples under optimised conditions we carried out a seedling emergence experiment in a climate room. For this purpose, rabbit dung was collected in February 2008 nearby the exclosure system. To analyse the content of available seeds we used the method according to Wessels & Schwabe (2008). In total 1920 g (dry weight) concentrated rabbit dung was divided into 48 samples (each 40 g dry weight) and dispersed on trays subsequently.

Trays were established in a climate room with a day/night air temperature of 20/5 °C (T_{max} = 27 °C) and 16 h light (PPFD 300-800 μmol $m^{-2}s^{-1}$) availability per day. Water was provided daily up to field capacity. The first run in the climate room took six weeks. After this, slightly moist samples were stratified for six weeks at a cold house with an air temperature of 0-4 °C. The last run in the climate room took another six weeks. Seedling emergence was recorded throughout with the help of determination literature (Hanf 1999; Muller 1978). Identified seedlings were removed; unidentified plants were transplanted into larger pots until determination was possible. As a reference we were able to compare the results with data from the year 2001 under low rabbit impact with the same methodical approach (Jährling 2003).

In addition, we determined the above-ground phytomass production and extraction rates by rabbits in 2006 and 2007 by comparison of mini-exclosures (1 m x 2 m) and side-by-side comparative plots. Two mini-exclosures and comparative plots were arranged adjacent to each of the 6 rabbit split-plots. Clipping was done every 4 to 6 weeks by an electric clipper around the summer period (between May and October) up to a stubble-field height of about 2 cm on 5 harvest-times a year. The position of the plots was changed each time after the clipping. At this time the area was not grazed by sheep. Phytomass was separated into the PFTs “graminoids”, “legumes” and “other herbs”, dried for 48 h at 70 °C and subsequently weighed. The extraction rates were calculated by means of differences between the phytomass of

the ungrazed plots at the end of the harvest interval and the phytomass of the grazed plots at the beginning of the next interval.

Statistical analyses

Relevés were ordinated by means of detrended correspondence analysis (DCA) using PC-ORD 5.31 (NMDS led to very similar results which are not shown). The cover data were square-root transformed beforehand. The DCA was run with downweighting of rare species and rescaling; the number of segments was 26.

Mixed linear models (SAS 9.2, PROC MIXED, SAS Institute Inc., Cary, NC, USA; Littell et al. 2000) were calculated to assess the effects of grazing and year on various dependent variables (vegetation and community structure parameters: number and cover of plant species, number and cover of graminoid species, number and cover of herb species, number and cover of Fabaceae species, number and cover of cryptogams, number and cover of bryophytes, number and cover of species with growth height 1, 2 and 3, number and cover of Red Data species, number and cover of annual and perennial species, cover of bare ground, cover of litter, TSR, both turnover-ratios; the cover of the 29 plant species which reached a degree of presence at least 40 %; number of flower units, number of flowering species, number of produced fruits, aboveground phytomasses of graminoids, herbs and legumes).

In a first run, the reference year (2000) of the long-term dataset from SR and R plots was tested separately to reveal possible differences of the first year. If there were no differences, we used the remaining years (2001-2009) for further analyses. In addition, the dataset of SR, R and N plots from 2005-2009 was put in a separate analysis. Again, values were square-root transformed before calculating mixed linear models if necessary.

Allowing comparisons of several covariance structures, mixed linear models are especially applicable for analyzing repeated-measures data (Littell et al. 1998). The most commonly used structures are (according to Littell et al. 2000): autoregressive, compound symmetry and unstructured. Additionally we included: autoregressive heterogeneous, compound symmetry heterogeneous, autoregressive moving-average and Huynh-Feldt. These seven covariance structures were compared according to goodness-of-fit criteria as suggested by Littell et al. (2000). We chose the corrected Akaike criterion (AICC) as guideline (Fernández 2007), but structures which did not comply with basic assumptions (e.g., homogeneous variances) were dismissed in some cases. If two structures led to equal AICC values, the simpler structure was chosen (Kincaid 2005). For the calculation of degrees of freedom, we selected the Kenward-Roger approximation as recommended by Schaalje et al. (2001, 2002) and Arnau et al. (2009). Vallejo et al. (2004) and Jacqmin-Gadda et al. (2007) were able to show that mixed linear models using this method are robust against deviation from normal distributions in terms of both error control and power. Nevertheless, the

studentised residuals and conditional studentised residuals were examined for normality by means of graphical display (histograms and quantile-residuum plots); a nearly Gaussian distribution could be ascertained.

Tukey-adjusted post hoc tests were carried out to test for grazing effects within single years and grazing types.

Results

General observations

The investigated area was separated into plots with typical Armerio-Festucetum stands and plots with more ruderalised vegetation according to the first DCA-axis (Fig. 3.2). Species which are mainly present in the typical plots on the left side are e.g., *Koeleria macrantha, Carex praecox*, *Cladonia furcata* s.l.; *Poa angustifolia, Carex hirta* and *Cynodon dactylon* are characteristic for the ruderalised plots on the right side.

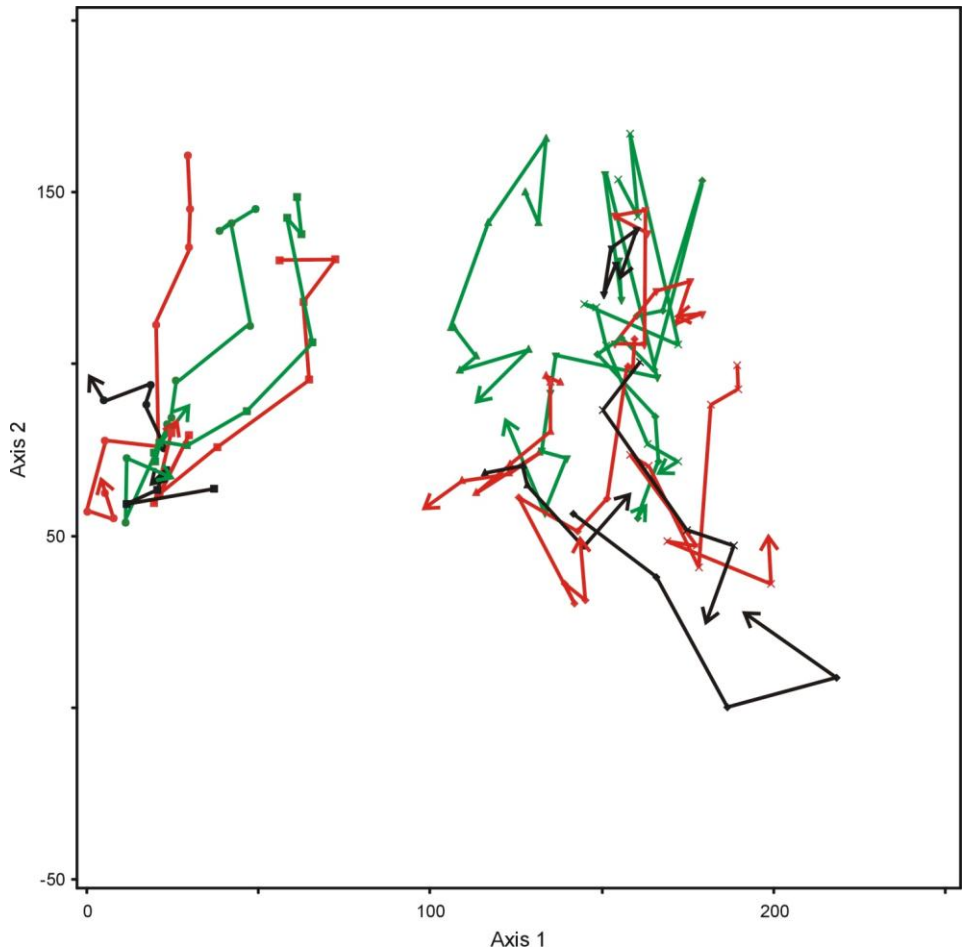


Figure 3.2: Development of the plots (DCA). Green: SR (2000-2009), red: R (2000-2009), black: N (2005-2009). Left side: plots in typical Armerio-Festucetum vegetation, right side: plots in slightly ruderalised Armerio-Festucetum vegetation. The time points of each plot type have been connected by trajectories, arrowheads: year 2009. Axis 1: eigenvalue 0.28, gradient length 2.2 SD; axis 2: eigenvalue 0.10, gradient length 1.7 SD; axis 3: eigenvalue 0.08, gradient length 1.8 SD. Axes are scaled in 1 SD = 100.

The temporal development of the plots can be reconstructed along axis 2. Especially in the years 2000-2004 there is a strong development downwards along the second axis, with longer steps from 2002 to 2003 and from 2003 to 2004. Since 2005, no development but rather stability can be recognised on the typical plots. Additionally, the more ruderalised plots show an irregular course in case of the R and SR plots and there are no clear successional trajectories. In contrast, two ungrazed plots - one with dominance of *Carex hirta*, the other one with *Cynodon dactylon* - show relatively long trajectories and an increase of these ruderal graminoids.

The turnover ratios of SR and R plots in Fig. 3.3a were very similar and show two peaks, one in the years 2003 and 2004 (ca. 30-35 % species turnover) and a second one, mainly in the years 2006 till 2008 (ca. 25-30 % species turnover). The second peak was a bit smaller on R plots (ca. 23 %) than on SR plots (ca. 30 %). N plots revealed a species turnover peak in 2007 (ca. 30 %) whereas ratios remained in 2009 at higher levels (ca. 25 %) than on SR and R plots (ca. 15 %). Three species newly emerged on N plots in 2009: *Calamagrostis epigejos*, *Phleum phleoides* and *Prunus serotina*. Statistical tests of the years 2005-2009 of SR, R and N plots (Tab. 3.2) showed a slight dependence of the interaction term "grazing*year" ($p=0.0412$). According to Tukey-adjusted post hoc tests, differences between N and SR plots in 2009 are significant ($p=0.0157$).

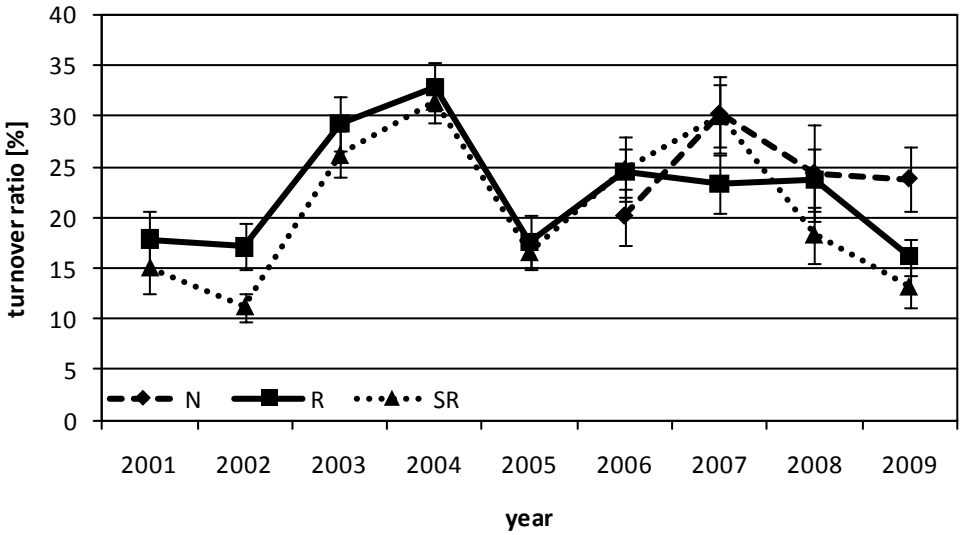


Figure 3.3a: Mean turnover ratio between two years (2000/2001; 2001/2002; ...) ± standard error.

The turnover ratio on SR and R plots regarding the reference year 2000 (Fig. 3.3b) revealed a small peak in 2003 (almost 30 %) and a bigger second peak beginning in 2006 and ending in the years 2007 and 2008 (both years with a species turnover of about 40 %) which is evidence for higher rabbit grazing activities. In 2009 turnover ratios were lower on both plot types, with values of about 25 %. This

means that the last year partly approximates the reference year 2000 with a similar species ratio. Species which have recovered in 2009 are for instance *Carduus nutans*, *Cerastium semidecandrum*, *Silene conica* and *Potentilla recta*.

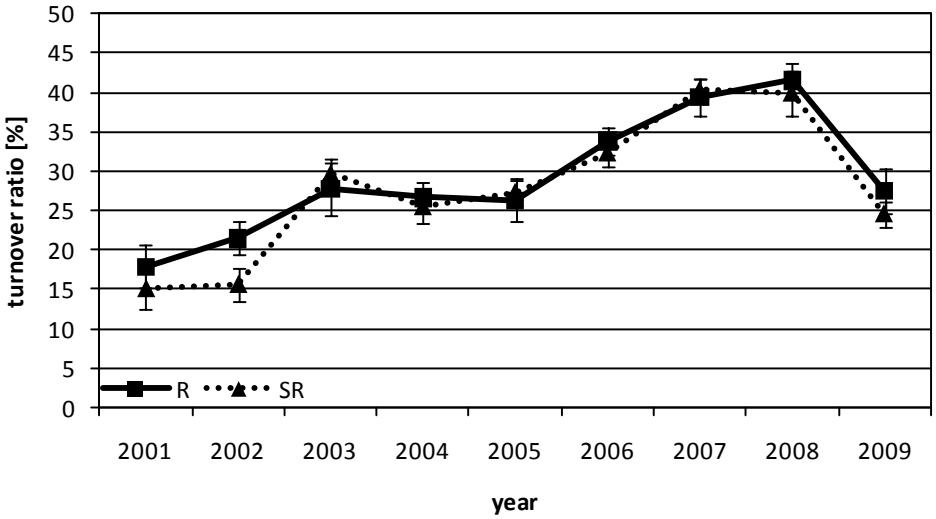


Figure 3.3b: Mean turnover ratio regarding the reference year 2000 ± standard error.

Table 3.2. Results of the SAS mixed-linear model analysis regarding the years 2005-2009 (plot types SR, R and N). Only significant effects are shown. Num df: degrees of freedom Numerator, Den df: degrees of freedom Denominator, p: level of significance.

Effect	Num df	Den df	F value	p
Turnover ratio				
Year	3	13.0	5.97	0.0087
Grazing*year	6	16.0	2.91	0.0412
Total species number				
Year	4	12.0	59.08	<0.0001
Grazing*year	8	15.4	3.60	0.0150
Number of species growth height 3 (> 50 cm)				
Year	4	60.0	13.63	<0.0001
Grazing*year	8	60.0	2.84	0.0095
Cover of bryophytes				
Year	4	32.8	4.60	0.0046
Grazing*year	8	38.0	2.98	0.0108
Cover of litter				
Year	4	12.0	8.30	0.0019
Grazing	2	15.0	9.99	0.0017
Grazing*year	8	15.4	4.92	0.0037

Biotic disturbance at a low level:
Extensive sheep grazing at low rabbit population densities; years 2000-(first half) 2005

The pre-grazing state on the additional permanent plots showed almost constant species numbers (± SE) with a mean of 24.0 ± 2.7 species per 25 m² in the year 1999 and, after extensive sheep grazing started, 23.0 ± 1.6 species in the year 2000. The development of the total species numbers of the other plot types is depicted in Fig. 3.4. Species numbers on SR and R plots (n = 12) were almost stable with exception of the year 2003. They showed a mean of 38.1 ± 1.3 species per 25 m² in the year 2000 and 37.8 ± 0.0 species in 2004. Statistical analysis showed effects only of the factor "year" (p=0.0006; Tab. 3.3). Grid plot data showed very similar results. With a mean of 43.0 ± 2.1 species in 2000 and 44.6 ± 2.2 species in 2004 there were only minor changes.

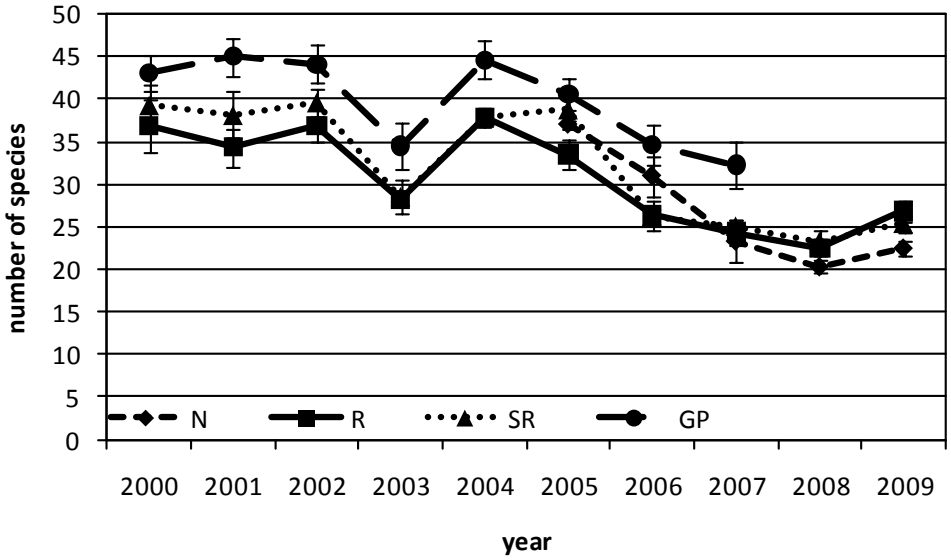


Figure 3.4: Mean number of plant species of the plot types SR, R, N (each 25 m²) and additionally gridplots (GP; each 79 m²) ± standard error.

Changes in vegetation structure can be detected in case of growth height 3 (Fig. 3.5). These are tall plants (> 50 cm) like *Asparagus officinalis*, *Carduus nutans*, *Centaurea stoebe* s.l., *Sisymbrium altissimum* or *Verbascum phlomoides*. There were more tall species without sheep grazing in 2001, 2002 and 2003. The slicing option revealed significant differences between SR and R plots in 2003 (p=0.0117). Grazing leads to a decline in the cover of graminoids in case of *Agrostis capillaris*, *Poa angustifolia* and *Elymus repens*. SR plots showed a lower graminoid cover than plots with only rabbit grazing. The cover of *Carex hirta* decreased on SR plots till 2003 but slowly increased afterwards whereas the cover of *Carex* on R plots increased from 5 % in 2000 up to 12 % in 2003. In case of *Cynodon dactylon* cover values never exceeded a level of about 10 % on SR as well as on R plots.

Table 3.3: Results of the SAS mixed-linear model analysis regarding the years 2000-2005 (plot types SR and R). Only significant effects are shown. Num df: degrees of freedom Numerator, Den df: degrees of freedom Denominator, p: level of significance.

Effect	Num df	Den df	F value	p
Total species number				
Year	8	6.0	25.06	0.0006
Turnover ratio				
Year	8	3.0	10.18	0.0412
Turnover ratio (regarding 2000)				
Year	8	67.0	31.10	<0.0001
Number of species growth height 3 (> 50 cm)				
Year	8	3.0	12.22	0.0319
Grazing*year	8	3.0	11.88	0.0332
Cover of bryophytes				
Year	9	32.3	7.94	<0.0001
Grazing*year	9	32.3	3.21	0.0069
Cover of litter				
Year	9	17.8	7.99	0.0001
Grazing	1	11.5	25.06	0.0003
Grazing*year	9	17.8	2.59	0.0418

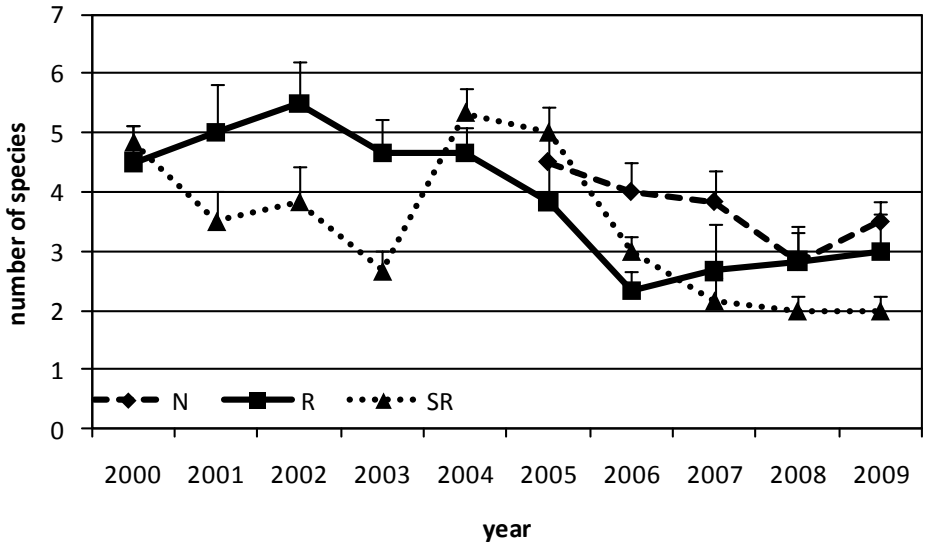


Figure 3.5: Mean number of plant species with growth height 3 (GH3; > 50 cm) ± standard error. SE only one-sided.

The cover of bryophytes increased on SR and R plots in the first years with exception of the year 2003 (Fig. 3.6) but the increase of cover was faster and higher on R plots. The interaction term "grazing*year" is significant (p=0.0069) and slicing showed significant differences between the two plot types in 2004 (p=0.0212).

The cover of the litter layer (Fig. 3.7) was the only investigated variable which showed significant differences between SR and R plots nearly throughout the whole study ("grazing" p=0.0003; interaction term "grazing*year" p=0.0418; see Tab.

3.3). Nevertheless, there were already differences between both plot types regarding the reference year 2000. Slicing showed significant differences between the plots in the years 2000 to 2004. Anyhow, litter cover on SR plots as well as on R plots doubled comparatively but at different levels. Hence, litter cover never exceeded about 10 % on the SR plots. This was in contrast to R plots, which showed an increase in cover of about 50 % in 2003. Thereafter, values strongly decreased on both plots until 2005 (cover below 5 % on SR and below 20 % on R plots) and increased again in the following years. However, there were already differences between both plot types regarding the reference year 2000.

The most obvious result concerning influences of sheep grazing is that no considerable effects were found. Neither species numbers nor community characteristics were changed in any important way.

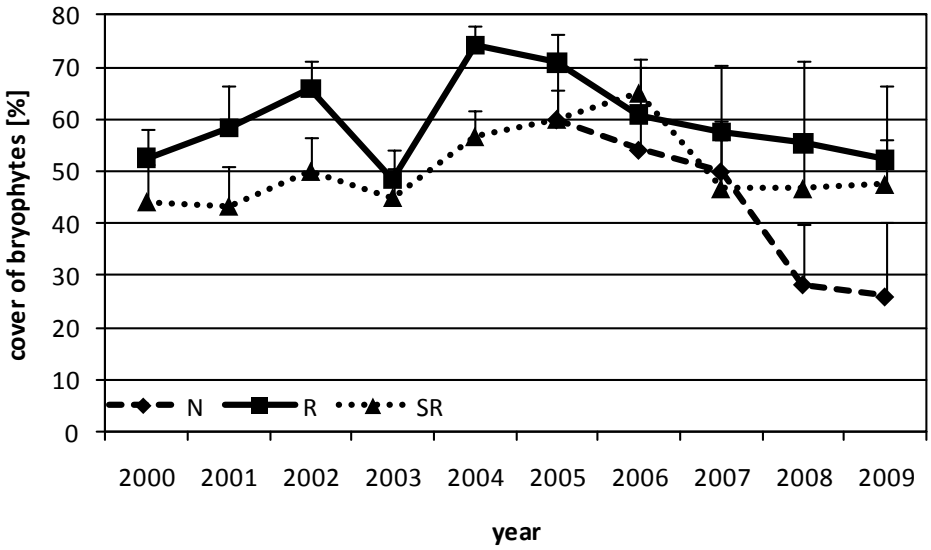


Figure 3.6: Mean cover of bryophytes [%] ± standard error. SE only one-sided.

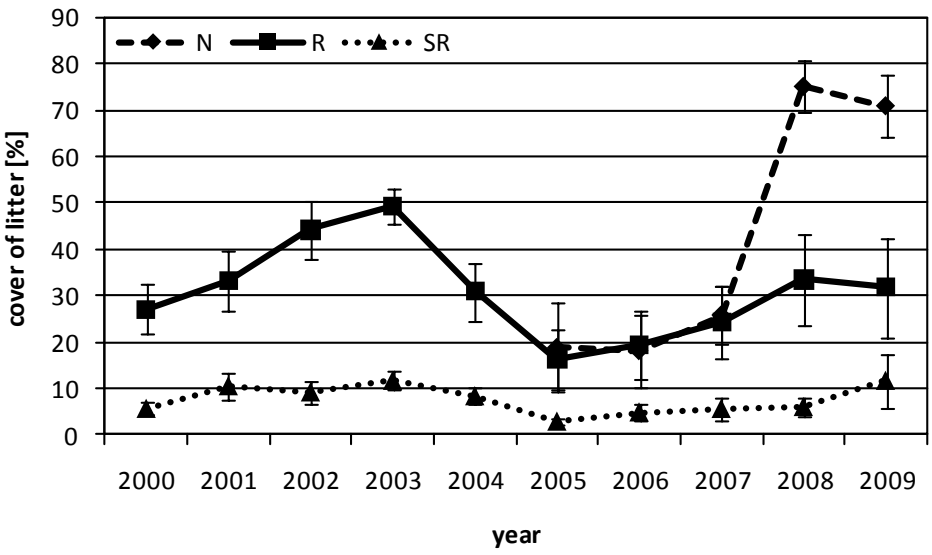


Figure 3.7: Mean cover of litter [%] ± standard error.

Abiotic disturbance: severe drought in 2003

The decline of species numbers in the dry year 2003 was conspicuous and demonstrated for all plot types (Fig. 3.4). This year showed the highest duration of sunshine of all investigated years and also the lowest amount of precipitation (Fig. 3.1). The special quality of this year was also obvious in the turnover ratio, which reached a peak in 2003 with a species turnover of about 30 % (Fig. 3.3a). Species numbers (± SE) decreased by about 10 species, from 38.3 ± 1.4 species in 2002 to 28.3 ± 0.2 species in 2003, on SR and R plots and increased by about 10 species to 37.8 ± 0.0 species in 2004. The development of the species numbers on GP plots was similar: they showed a decrease from 44.1 ± 2.3 species in 2002 to 34.5 ± 2.8 species in 2003 and an increase to 44.6 ± 2.2 species in 2004.

The low species numbers of all plots in 2003 result from the decline of mainly therophytes like *Arenaria serpyllifolia*, *Cerastium semidecandrum*, *Medicago minima*, *Myosotis ramosissima* and *M. stricta*, *Silene conica* or *Trifolium campestre*. The breakdown of annual species primarily concerns Koelerio-Corynephoretea species. Annuals in other classes like Festuco-Brometea or Molinio-Arrhenatheretea showed only a slight species decline instead. Furthermore, these classes contain most of our investigated perennial plant species.

Even bryophytes and perennial grass species show a response due to drought. Cover values of *Poa angustifolia* strongly decreased from about 30 % in 2002 on R plots to 12 % in 2003 and actually to 5 % in 2004. The effect on SR plots was similar. There was also a drastic decrease of cover values of *Cynodon dactylon* (from 10 % in 2003 to 2 % in 2005 on both plot types). Since 2006 *Cynodon* was able to recover quickly. The decrease of the cover of bryophytes was predominantly visible on R plots. Values decreased there from 65 % in 2002 to 50 % in 2003 but strongly increased in 2004 up to 75 %.

Extended approach: intensive rabbit grazing; years 2005 (second half)-2009

Plant community and vegetation structure

Species numbers (Fig. 3.4) decreased from 36.2 ± 2.7 species in 2005 to a minimum of 22.8 ± 0.3 for SR and R plots in 2008. The species number was slightly higher in 2009 with 26.1 ± 0.8 species. Species which were not present in 2008 on R plots but were there in 2009 include, e.g., *Bromus tectorum*, *Cerastium semidecandrum*, *Medicago minima*, *Myosotis ramosissima*, *Potentilla recta* or *Vulpia myuros*, and on SR plots: *Myosotis stricta*, *Silene conica*, *Senecio jacobaea* or *Polygonum aviculare*. The ungrazed N plots started in 2005 with 37.0 ± 0.6 species per 25 m² and showed the lowest species numbers in 2008 (20.3 ± 0.8). There was also a slight increase in species numbers (22.5 ± 0.8) on N plots in 2009; this was

caused by the following species, e.g. *Calamagrostis epigejos*, *Centaurea stoebe* s.l., *Phleum phleoides* or *Sisymbrium altissimum*. Statistical analysis (see Tab. 3.3) showed effects of the factor "year" ($p<0.0001$) and of the interaction term "grazing*year" ($p=0.0150$). Tukey-adjusted post hoc tests revealed a significant difference between R and N plots in 2009 ($p=0.0322$). Again, results on GP plots were very similar. Species numbers declined on the grid point plots since 2005, too. The decline of species numbers on all plots can be observed throughout all investigated groups and plant functional types, and is therefore characteristic for the whole investigation. Furthermore, only effects of single years were significant regarding more or less most variables.

The cover of bryophytes began to decrease in the last years of the study (Fig. 3.6). This occurred on R plots in 2005, and on SR plots two years later in 2007. The decline was very drastic on N plots and the cover decreased from 60 % in 2005 to nearly 25 % in 2009. Statistical tests showed an interaction of "grazing*year" ($p=0.0108$) but Tukey-tests were insignificant afterwards.

The cover of litter (Fig. 3.7) increased on every plot type since 2005 and has doubled on R (from 15 % to 30 %) and SR plots (from 5 % to 10 %) and nearly quadrupled on N plots (from 20 % to 70 %). There was a significant impact of grazing ($p=0.0017$) and the dependence of the year is shown by the interaction term "grazing*year" ($p=0.0037$) (Tab. 3.3). Slicing and Tukey-adjustments showed significant differences between all three plot types in 2008 and 2009.

The great increase of litter on plots without grazing was in contrast to the cover of bare ground soil, which decreased on N plots since this plot type was established in 2005, from 5 % to nearly 0 %. It increased from 1-2 % on SR and R plots throughout the years up to 7-9 % in 2006, but since then these values have also decreased on R plots. The cover on SR plots remained at the higher level with exception of 2009, when there was a slight decrease from about 10 % to 6 %.

Flower phenology, flower production, seed production and seed content in faeces

Fig. 3.8 shows the flower phenological phases during the three investigated years. There were large differences between the years regarding flower abundances on N and R plots, but shifts in phenological phases due to rabbit grazing were not observed. Flowering phases in spring and early summer were particularly generated by species like *Carex hirta* and *Cerastium arvense*.

Midsummer flowering was dominated by *Medicago falcata* (incl. *M.* x *varia*), but these flowered abundantly on rabbit-free plots only. Furthermore, *Rumex acetosella* s.l. produced large amounts of flowers on N plots in more typical stands of the Armerio-Festucetum, just as *Potentilla argentea* agg. produced them in the ruderalised parts.

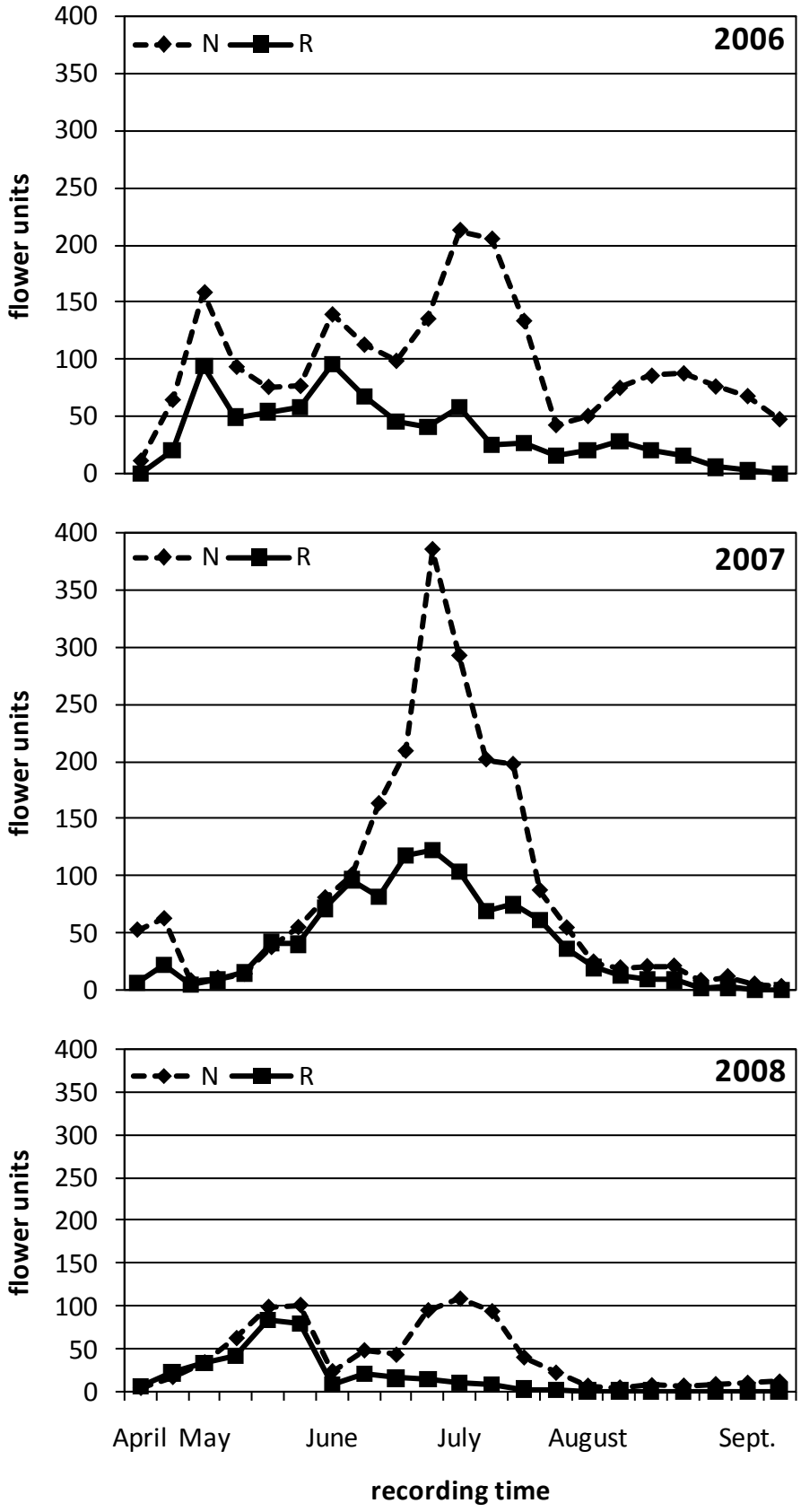


Figure 3.8: Mean number of flower units and flower phenology per 1 m². Error bars are not depicted to ensure readability.

Flower units were visibly reduced on R plots. Fig. 3.9 shows the mean of flower sums as estimated on N and R plots: the reduction by grazing was significant ($p=0.0145$), as well as the impact on the maxima of flowers on R plots ($p=0.0171$). Furthermore, the effects of grazing on the number of flowers and the numbers of flowering plant species (Fig. 3.10; Tab. 3.4), counted at the different recording times during a recording year, were highly significant ($p<0.0001$).

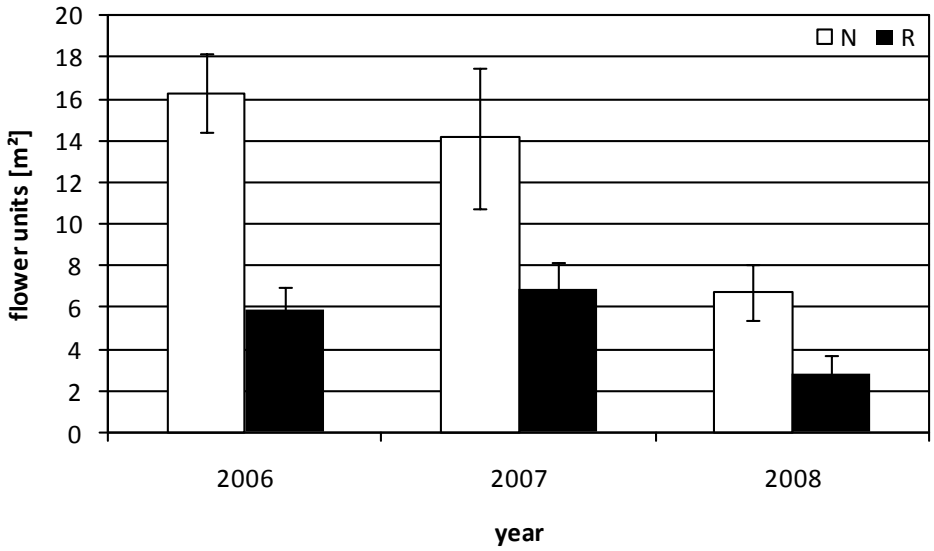


Figure 3.9: Flower units (sum) per 1 m² ± standard error.

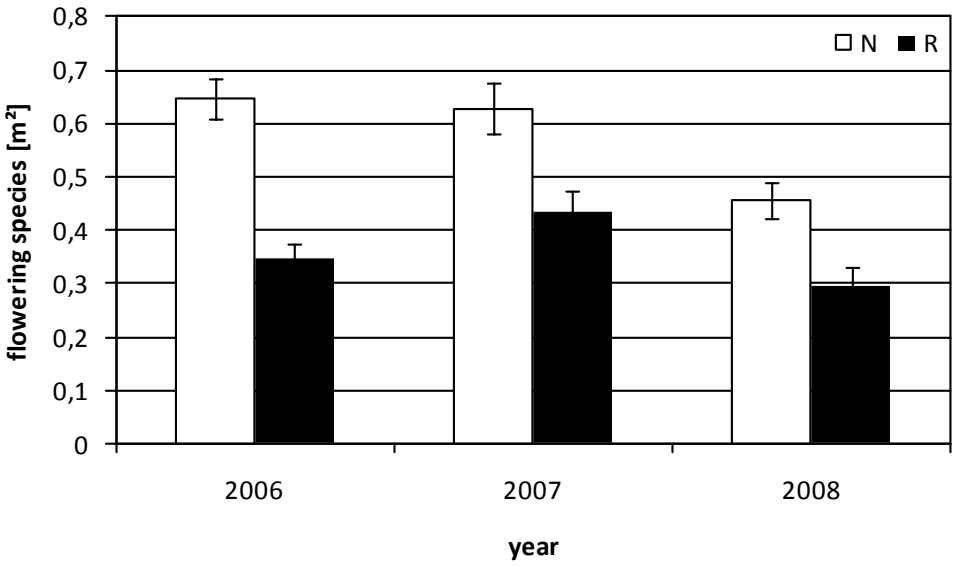


Figure 3.10: Flowering species per 1 m² ± standard error.

The grazing impact on the flower production of many plant species was in most cases not significant because the plots varied so widely (Tab. 3.4). Hardly any flowering individuals of *Armeria maritima* ssp. *elongata* or *Silene latifolia* ssp. *alba* were present on R plots. Inflorescences of *Verbascum phlomoides* were rather rare on R plots. The grazing impact on *Verbascum phlomoides* flowers depended on the year,

so the interaction term "grazing*year" was significant (p=0.0027). Only *Erodium cicutarium* agg. and *Geranium molle* showed higher flower numbers on R plots. Regarding *Erodium* this was particularly obvious in 2007. The grazing effect was dependent on the year (interaction term "grazing*year" p=0.0168) which was similar to *Geranium* ("grazing*year" p=0.0392).

Table 3.4: Results of the SAS mixed-linear model analysis regarding the extended approach (plot types R and N). Only significant effects are shown. Num df: degrees of freedom Numerator, Den df: degrees of freedom Denominator, p: level of significance.

Effect	Num df	Den df	F value	p
Number of flowers (sum)				
Year	2	17.5	4.22	0.0320
Grazing	1	20.1	7.16	0.0145
Number of flowers per recording time				
Year	2	84.3	13.24	<0.0001
Grazing	1	119.0	27.67	<0.0001
Number of flowers (maxima)				
year	2	9.0	29.45	0.0001
grazing	1	10.0	8.15	0.0171
grazing*year	2	9.0	16.30	0.0010
Number of flowering species per recording time				
Year	2	84.6	9.23	0.0002
Grazing	1	125.0	48.28	<0.0001
Number of flowers of single plants species				
Reduction on R plots:				
Verbascum phlomoides				
Year	2	20.0	8.06	0.0027
Grazing	1	10.0	7.85	0.0187
Grazing*year	2	20.0	8.06	0.0027
Increase on R plots:				
Erodium cicutarium agg.				
Year	2	9.0	10.55	0.0044
Grazing*year	2	9.0	6.66	0.0168
Geranium molle				
Year	2	9.0	25.07	0.0002
Grazing*year	2	9.0	4.74	0.0392
Phytomass reduction (total)				
Year	1	178.0	47.54	<0.0001
Grazing	1	178.0	19.46	<0.0001
Grazing*year	1	178.0	5.04	0.0260
Phytomass reduction of PFTs:				
"Graminoids"				
Year	1	58.0	53.23	<0.0001
Grazing	1	58.0	37.79	<0.0001
"Legumes"				
Grazing	1	58.0	16.48	0.0001
"Other herbs"				
Year	1	58.0	73.95	<0.0001
Grazing	1	58.0	16.49	0.0001
Grazing*year	1	58.0	21.42	<0.0001

Rabbit grazing affected the seed production of all analysed species (Tab. 3.5). Six species produced fewer fruits and two species produced more fruits under rabbit grazing. *Erodium cicutarium* agg. was the only species with a statistically significant increase of fruits in the case of R plots ("grazing" p=0.0156).

Species	N	R	p
Armeria maritima ssp. *elongata**	183 ± 116	3 ± 2	n.s.
Erodium cicutarium agg.	9 ± 6	121 ± 56	0.0156
Geranium molle	58 ± 45	200 ± 80	(0.0739)
Medicago falcata (incl. *M.* x *varia*)	7812 ± 4574	1480 ± 1478	(0.0898)
*Medicago minima**	7 ± 6	6 ± 3	n.s.
Potentilla argentea agg.	1138 ± 777	270 ± 119	n.s.
Sedum acre	299 ± 299	83 ± 53	n.s.
Silene latifolia ssp. *alba*	193 ± 115	18 ± 13	n.s.

Table 3.5: Mean seed production per m² (± standard error) in 2007. * = "Red Data" (Germany; Korneck et al. 1996). p = level of significance; parentheses = slightly not significant (p < 0.10).

Rabbit dung samples (Tab. 3.6) showed a total of 13 seedlings per 100 g air-dry faeces emerging from dung samples (mean number: 0.534 ± 0.081); these represent 16 taxa. The main species in rabbit dung was *Solanum nigrum*, with a percentage of 83 % (208 seedlings).

Generally, annual species accounted for the main percentage in the dung (56 %), and the percentage of emerged annual individuals was even higher (94 %). Compared to 2001 the seed content was much lower and poor in target species (2001: 9, 2008: 4); the portion of allochthonous species was higher in 2008 (Tab. 3.6). After stratification 22 % of the total number of seedlings newly emerged from the dung comprised two new species: *Fragaria* x *ananassa* and *Plantago major*. Beside the above mentioned species we found another three allochthonous species in the dung: *Amaranthus retroflexus*, *Portulaca oleracea* and *Robinia pseudoacacia*.

Plant Functional Types: phytomass extraction

Comparison of the two examined years reveals a remarkably high phytomass productivity in the year 2007 (Fig. 3.11). Values of single PFTs have more than doubled. Generally, the main rabbit diet consisted of grasses. Depending on the year, 52-65 % of "graminoids" were consumed by rabbits. The extraction was highly significant ("grazing" p<0.0001; Tab. 3.4). Phytomass reduction was even higher in the fraction of "legumes" and "other herbs". Up to 95 % of the legume phytomass ("grazing" p=0.0001) and 85 % of the other herbs' phytomass ("grazing" p=0.0001) were reduced. It seems worth mentioning that the overall phytomass reduction in the Armerio-Festucetum was 58-70 % and thus statistical tests showed that the grazing impact by rabbits was highly significant ("grazing" p<0.0001).

Table 3.6: Mean content of viable seeds per 100 g air-dried faeces in the experiment in the climate room (year of sampling: 2008) compared with an emergence experiment from Jährling (2003; year of sampling: 2001). Parentheses: 95 % confidence interval.

Year	2001		2008	
Total dry weight of faeces [g]	821		1920	
No. of samples	45		48	
Target species Armerio-Festucetum				
Potentilla argentea agg.	0.018	(0.013)	0.009	(0.004)
Rumex acetosella s.l.	0.031	(0.023)	0.004	(0.003)
Arenaria serpyllifolia agg.	0.008	(0.011)	0	
Cerastium semidecandrum	0.016	(0.022)	0	
Corynephorus canescens	0.005	(0.007)	0	
Saxifraga tridactylites	0.003	(0.005)	0	
Silene conica	0.003	(0.005)	0	
Silene otites	0.005	(0.007)	0	
Thymus pulegioides	0.003	(0.005)	0	
Erodium cicutarium agg.	0		0.004	(0.003)
Medicago minima	0		0.004	(0.003)
Non-target species				
Chenopodium album	0.031	(0.028)	0.006	(0.004)
Chenopodium strictum	0.003	(0.005)	0.009	(0.005)
Herniaria glabra	0.065	(0.050)	0.004	(0.003)
Poa angustifolia	0.034	(0.023)	0.002	(0.002)
Verbascum phlomoides	0.514	(0.134)	0.004	(0.003)
Agrostis capillaris	0.005	(0.010)	0	
Carex hirta	0.003	(0.005)	0	
Cerastium holosteoides	0.021	(0.037)	0	
Conyza canadensis	0.026	(0.022)	0	
Galium album	0.003	(0.005)	0	
Oenothera biennis s.l.	0.036	(0.023)	0	
Psyllium arenarium	0.010	(0.010)	0	
Setaria viridis	0.008	(0.009)	0	
Taraxacum spec.	0.008	(0.009)	0	
Veronica arvensis	0.018	(0.020)	0	
Eragrostis minor	0		0.015	(0.006)
Allochthonous species				
Fragaria x *ananassa*	0.018	(0.015)	0.002	(0.002)
Epilobium spec.	0.003	(0.005)	0	
Amaranthus retroflexus	0		0.004	(0.003)
Plantago major	0		0.002	(0.002)
Portulaca oleracea	0		0.015	(0.005)
Robinia pseudoacacia	0		0.006	(0.005)
Solanum nigrum	0		0.442	(0.073)
Total content of seeds	41		13	
Total no. of species	26		16	
Total no. of individuals	335		251	
TSR_{qual} [%]	13.9	(5.7)	8.5	(6.0)

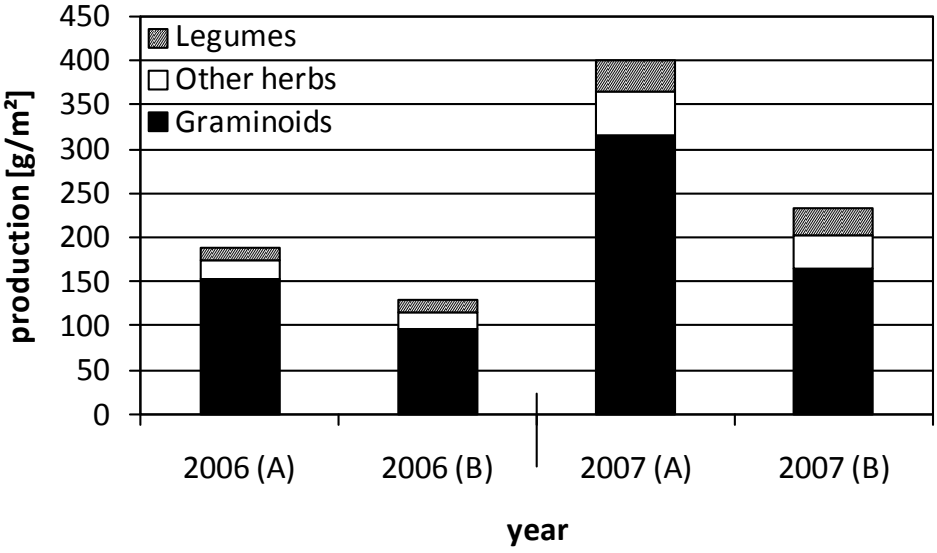


Figure 3.11: Total aboveground phytomass production (A) and extraction (B) by rabbits [g/m² dry weight] between May and October.

Discussion

General remarks

For most variables grazing effects concerned only single years or were not significant. Interannual changes affected grazed plots and ungrazed plot types equally, as was also observed by Wesche & Retzer (2005) in the extreme system of the Mongolian steppe. Due to the heterogeneity of the vegetation with typical and ruderalised subtypes, we were often unable to reveal significant grazing impacts in statistical tests. In spite of all the different levels of disturbance severities, our results document an ecosystem with great potential for recovery and therefore resilience, illustrated by a conceptual model in Fig. 3.12. The buffering effect of our community is consistent with the insurance hypothesis by Yachi & Loreau (1999), which suggests that biodiversity insures ecosystems against declines in their functioning. Bruelheide & Luginbühl (2009) disagree about putative positive effects of species number on stability and assume that these might have been counterbalanced by a disruption of niche complementarity in species-rich communities. Trubina (2009) concluded that the resilience of communities does not exclusively depend on species richness. In addition, resilience depends on the degree of disturbance (Allison 2004; Bruelheide & Luginbühl 2009; Trubina 2009) and as hypothesised by Dynesius et al. (2009) resilience is influenced by spatial variations in stress and resource availability, the number of disturbance-intolerant species and ultimately by the magnitude of environmental changes brought about by a disturbance with a specific intensity.

Moderate disturbance (sheep grazing)

At first, we assumed that changes in species numbers and diversity are particularly connected with the change from a mowing or mulching to a grazing regime. The "nature-in-flux paradigm" hypothesises that patterns of change in an ecosystem are influenced by its past (Urbanska 2000). The results of the additional permanent plots have shown that species diversity did not change due to the introduction of a grazing regime. Furthermore, it was obvious that extensive sheep grazing at our site can be an effective method to maintain diversity (see species number in Fig. 3.4 and conceptual model in Fig. 3.12). This was also shown by the ordination diagram which revealed that plots under moderate grazing intensities were very close together between 2000 and 2003. Besides, the study shows that sheep grazing reduced tall-growing plant species and that primarily sheep-grazed plots have a lower litter cover and a higher percentage of bare ground, which is consistent with Eldridge & Myers (2001), Croft et al. (2002) or Hellström et al. (2003). We assume that these sites can maintain their structure due to positive related disturbance effects, which are in particular grazing and trampling in moderate intensities.

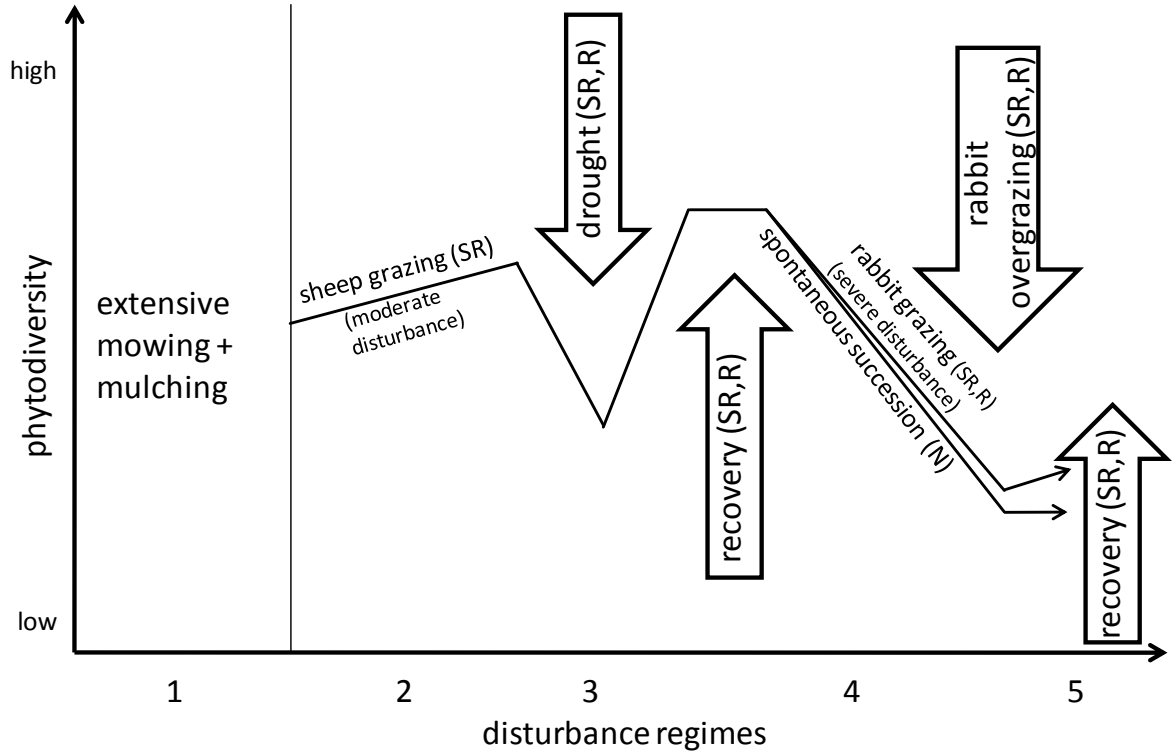


Figure 3.12: Conceptual model showing the response of phytodiversity for five disturbance regimes. Further explanations: see text.

Hellström et al. (2003) observed in a study with sheep-grazed and ungrazed plots in semi-natural grasslands in Finland an increase of species numbers by nearly 30 % in case of sheep grazing. Our findings suggest that this may apply only if there are no

further, stronger disturbance effects like high rabbit densities in the community, which are able to counteract the positive impact of sheep grazing. The grazing-reversal hypothesis suggests that grazing reduces plant diversity in unproductive habitats (Proulx & Mazumder 1998; Cingolani et al. 2005). Our study shows that species diversity strongly depends on grazing intensities. Römermann et al. (2009) have shown in calcareous grasslands in southwest Germany that grazing was the only management treatment compared to mowing, mulching or succession which is appropriate to sustain typical disturbance dynamics of species-rich semi-natural grasslands. Moreover, only grazed sites were in 'floristic equilibrium', which means a habitat can maintain its functional characteristics due to altered management. Kahmen et al. (2002) also observed in calcareous grasslands in south Germany that sheep grazing as a conservation management tool leads to variations in species and trait composition compared to burning or fallow, which are not recommended for management purposes. Furthermore, the vegetation dynamic is higher and more species may colonise by seeds. An experiment by Marriott et al. (2009) in Scottish grasslands indicates slow changes in species composition due to extensive (sheep) grazing compared to intensive grazing, too. Additionally, they found an increase in species diversity compared to intensive grazing.

Severe abiotic disturbance (drought)

The drought in 2003 was an extreme environmental event predominantly in temperate Europe (Beniston 2004; Rebetez et al. 2006; Jentsch et al. 2007). Species richness in grasslands can vary substantially from year to year in relation to rainfall and can be strongly reduced by drought (Tilman & El Haddi 1992). Its impact led to a noticeable decline of species numbers or a decrease in cover values. In this extraordinary year moist weather conditions in winter and dry conditions in spring caused an absence or severe decline of predominantly therophytes and legumes on our plots. Cover values of graminoids decreased on our plots, too, but this happened in some cases not in 2003 but in 2004 (e.g., the C_4 invader *Cynodon dactylon* decreased mainly in 2004 and 2005 on our plots. This may be a late effect of the summer drought in 2003 and related to exsiccation of its rhizomes). Moreover, climatically extreme conditions may periodically lower population densities and thus increase the probability of extinction for rare species (Tilman & El Haddi 1992).

Anyhow, drought had only minor impacts on the whole community structure as was shown by the DCA. Thus, the community was stable and able to recover completely in the following year, which confirms our hypothesis 2. Species reached their previous level and transiently absent taxa were found again. Cover values especially of therophytes even increased in some cases, which can possibly be interpreted as an over-compensatory phenomenon. The pronounced decline of the cover of bryophytes on R plots in 2003 and the strong recovery in 2004, respectively, are probably due to the underestimation of the cover caused by the drought in 2003.

As evidence for the insurance hypothesis van Ruijven & Berendse (2010) describe the enhancement of community recovery with diversity after drought in their sowing experiment on arable fields in the Netherlands. Gilgen & Buchmann (2009), however, conclude that the above-ground productivity of Swiss grasslands at sites with higher annual precipitation (>1000 mm yr^{-1}) seem to be better buffered against disturbance by drought than sites with lower annual precipitation.

Severe biotic disturbance (rabbit grazing)

High grazing impact became evident by changes species numbers and phytomass extraction rates. According to the latter, rabbits quite selectively extracted the Plant Functional Types “legumes” and “other forbs” compared to “graminoids”. We assume that rabbits are able to compensate times of low phytomass production levels in the Armerio-Festucetum by grazing in fields near the studied site (Faust et al. 2007). This was proved by seed contents of rabbit faeces with great importance of allochthonous species like *Fragaria* x *ananassa* and *Solanum nigrum* especially in the year 2008. Besides, cover values of bryophytes decreased on N plots as well as on the other plots. We suppose that these findings are due to different effects and depend on the plot type. The decline happened on one hand on both grazed plot types, which could be related to the lack of the plants’ ability to adapt to such intensive grazing as that of the rabbits, and on the other hand on ungrazed plots, which could be related to successional processes. Nevertheless, a grazing-induced decrease of bryophytes was also found by Austrheim et al. (2007).

As the succession on the plots with rabbits and the plots with sheep and rabbits was very similar, this is an indication for overgrazing due to rabbits. Besides, we suppose that the introduction of sheep grazing at our site facilitated the development of the rabbit population. This corresponds to a study of Bakker et al. (2009) in which rabbits were facilitated by cattle. Sheep grazing leads to lower vegetation canopies because they prefer taller plant species (Bakker et al. 2009). Thus, rabbits rely on their escape capabilities and can keep an overview of their observed habitat. Anyhow, the impact of sheep grazing appeared to be overlaid by the rabbits’ influence in our case and we suppose that the strong increase of the rabbit population caused the strong decline in species numbers. The species numbers and the turnover ratio clearly indicate that many previously lost or decreased species on grazed plots have returned or recovered in 2009. Many of those species are of the same ecological strategy type according to the databank of Klotz et al. (2002): they are ruderals or stress-ruderals respectively, like *Cerastium semidecandrum*, *Myosotis ramosissima*, *M. stricta*, *Medicago minima* or *Vulpia myuros*. The recovery is probably related to their capacity for successful reestablishment by regeneration from the soil seed bank after the decline of the rabbit population due to the moist winter and spring which favoured diseases. Hence, these findings indicate a high buffering ability of the ecosystem and therefore a high resilience (Fig. 3.12).

There was also a severe flower reduction by rabbit impact. For some species the rabbit impact was not significant, which can be explained by the wide variation of flower abundances within the studied plots. The destructive impact of rabbits on inflorescences (including the entire prevention of flowering of many plant individuals) was already described by Farrow (1917), Watt (1962) or Kiffe (1989). Grayson & Hassall (1985) noticed that rabbits affect phenology, too, which is in contrast to our results. Despite the marked reduction of flowers we were not able to detect any rabbit-induced shifts in phenology. However, the main flower aspect in midsummer, primarily determined by *Medicago falcata* (incl. *M.* x *varia*), is almost completely lacking under rabbit grazing, in addition to *Armeria maritima* ssp. *elongata*. Inflorescences of this characteristic species vanished on rabbit grazed plots. The flower production of *Armeria* recovered impressively after the rabbit decline in 2009. Concerning entomophilous plant species, the reduction of flowers was obvious in the period of high rabbit densities. In parallel, the diversity of wild bees regarding species numbers and numbers of individuals was much reduced (Beil et al. 2008).

Erodium cicutarium agg. was the only species which produced significantly higher numbers of seeds under rabbit grazing. This is related to the low or absent grazing intensity on the flowers of this species. Occasionally the rabbits seem to eat ripe capsules of *Erodium*, because it is apparently often dispersed in the peripheral zone of latrines or near warren entries at our site. The feeding impact on *Geranium molle* (and *Euphorbia cyparissias*) was also very slight, which might be due to pubescence or poisonous ingredients (e.g., Geraniol).

We suppose that the decline of diaspores in rabbit dung indicated by comparison of data from Jährling (2003) with the present data is due to the strong decline in flower numbers and seed production.

Lack of biotic disturbance (spontaneous succession)

Studies by Süss et al. (2004, 2010) in sand ecosystems of our area have demonstrated that the speed of succession is dependent on the vegetation type and nutrient availability. Hence, their permanent plots in low-successional stages of sand vegetation (Sileno-Cerastietum) on nutrient-poor soils were relatively stable for over 13 years. In contrast, vegetation stands on nutrient-rich soils can show a very fast development into ruderalised vegetation, whereas the cover of competitive graminoids can strongly increase within two years (Süss et al. 2010).

Ungrazed plots, especially after abandonment, show lower species numbers (compare Kahmen et al. 2002; Kahmen & Poschlod 2004) and an encroachment of monodominant grass species (Süss et al. 2004; Süss & Schwabe 2007). Beside the decline of species numbers on plots with sheep and rabbit exclusion, which have shown spontaneous succession, there was a significant increase of litter cover since 2006 shortly after the ungrazed plots were created due to fencing. The litter consisted mainly of the C_4 grass *Cynodon dactylon* (and partly of *Carex hirta*) in plots

of more ruderalised stands of the Armerio-Festucetum, which resulted from the strong cover increase of this vegetatively spreading species. On plots in the typical parts the cover increased due to the litter of the grass *Koeleria macrantha*. Many studies already have shown the negative influence of litter on regeneration and survival of plants or species richness (cf. Sydes & Grime 1981a,b; Weltzin et al. 2005). Likewise, Kahmen & Poschlod (2004) observed a decline in the number of species on their plots after abandonment. Furthermore, Kahmen et al. (2002) assess a negative change in species composition on fallow sites due to litter accumulation, advanced succession or the establishment of woody species. This is in line with Marriott et al. (2009), who found rapid changes in species composition but no effect on diversity after abandonment. The consequences of species loss may not be immediately visible, but it decreases ecological resilience to disturbance or disruption, which results in vulnerable ecosystems (Peterson et al. 1998).

Species which newly emerged or recovered in 2009 on N plots were mainly competitors, competitive ruderals or competitive stress-ruderals (according to Klotz et al. 2002), e.g. *Calamagrostis epigejos*, *Phleum phleoides* or *Sisymbrium altissimum*. The slight recovery of therophytes in spite of a lack of disturbance is perhaps caused by moister climatic conditions in 2009, which favoured the decomposition of litter and therefore changed microclimatic properties such as photosynthetically active radiation (Facelli & Pickett 1991). Additionally, soil humidity may also directly influence regeneration success by enhancing germination and establishment (Rydgren et al. 2004). Therefore, availability of water and light are the most crucial factors for seedling emergence as well as establishment success of our (small-seeded) sand vegetation. A correlation between higher seedling emergences of small-seeded species and low amounts of grass litter was also found by Donath & Eckstein (2010).

Conclusions

The conceptual model (Fig. 3.12) summarises the impact of five disturbance regimes and shows the resilience of the studied community. After the extensive mowing and mulching management (period 1) moderate disturbance by extensive sheep grazing (period 2) maintained phytodiversity and floristic structure. Severe short term disturbance like drought (period 3) had no lasting effects concerning the floristic structure. Period 4 with severe disturbance by rabbits shows that parameters such as species numbers or numbers of flowers and seeds were negatively affected. Despite the extreme rabbit impact the community structure was almost stable, and already showed a slight recovery after the decline of the rabbit population which occurred in period 5. This recovery is also proved by first results of the years 2010 and 2011. Ruderal communities are not as stable as typical ones but react irregularly in case of severe disturbances. Lack of disturbance favoured spontaneous succession (period 4) and shows results quantitatively similar to those of intensive rabbit grazing, but qualitatively recovery affected different ecological strategy types: on

ungrazed plots mainly competitors recovered, on grazed plots mainly stress-ruderals. Extensive grazing regimes are important and primarily necessary to preserve community structures and prevent successional processes in periods without extreme biotic or abiotic events.

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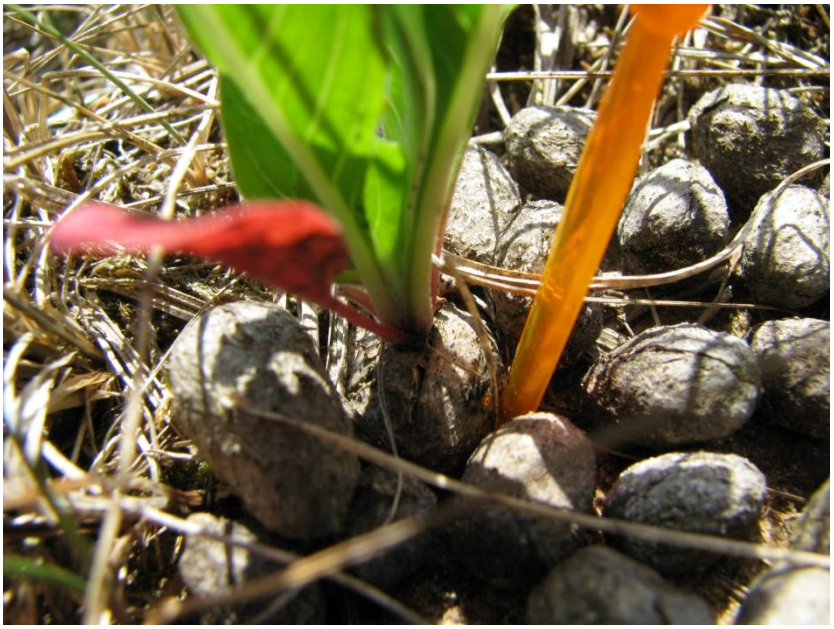
Post-dispersal impact on seed fate by livestock trampling – a gap of knowledge

Natural rabbit latrine at the study site
with dominance of *Salsola kali* and *Chenopodium album* agg.



Oenothera biennis s.l. seedling emerging out of sheep dung in the field experiment.

Abstract

Sheep grazing is an important management tool in threatened sandy grassland of the temperate zone. Besides direct grazing effects, previous studies have shown benefits of seed dispersal (epi-, endozoochory), but little is known about post-dispersal processes. We studied the role of sheep trampling for the post-dispersal fate of seeds embedded in sheep and rabbit dung and hypothesised a positive impact for the development of seedlings as a consequence of cracking the dung pellets. Sheep and rabbit dung samples were collected from species-rich sandy grasslands, and their seed potential was assessed in a climate room. In a factorial field experiment we tested the effects of trampling (using sheep-hoove replicas) and dung type on seedling emergence and fruiting success.

Seedling emergence in the field was only 5 % (sheep dung) or 7 % (rabbit dung) of the potential without trampling but 18 or 14 % with trampling. Plots with trampled sheep or rabbit dung both showed significantly more seedlings (3.6- or 2.1-fold), more species (2.4- or 1.9-fold), more fruiting individuals (3.9- or 2.6-fold) and more fruiting species (2.1- or 1.9-fold) compared to non-trampled dung plots. However, both target as well as non-target species profited from trampling. This is disadvantageous regarding nature conservation aims, but the proportion of target species is clearly increased by trampling and graminoid competitors did not reach fruiting stage.

Sheep play a multifaceted role in dispersal processes: after endozoochoric transport they act as a sort of ‘gardener’ not only for sheep-dispersed seeds, but also for those dispersed by rabbits.

Introduction

Seed dispersal and re-colonisation processes of plant individuals are decisive factors for population dynamics in grassland communities (Foster & Tilman 2003). In many open grazed habitats, herbivorous mammals transport large quantities of seeds of a broad range of vascular plant species both epi- and endozoochorously (e.g., Malo & Suarez 1995a, b; Milton et al. 1990; Fischer et al. 1996; Pakeman et al. 2002; Cosyns et al. 2005; Eichberg et al. 2007; Bakker et al. 2008). Recently, many studies focused on the potential role of herbivores to overcome seed limitations in a conservation and restoration context (Traba et al. 2003; Couvreur et al. 2004; Mouissie 2004; Wessels et al. 2008; Wessels-de-Wit & Schwabe 2010). By means of long-distance seed dispersal, moving livestock provides survival opportunities for small populations with a high extinction risk in fragmented landscapes (e.g., Bakker & Berendse 1999; Cosyns et al. 2005; Mouissie et al. 2005; Ozinga et al. 2009), but a potential threat to nature conservation aims by endozoochorous seed transfer has also been highlighted since non-target species are transported as well (Eichberg et al. 2007). A few studies have shown a positive relationship between dung seed content and species abundance in the vegetation (Bakker & Olff 2003; Cosyns & Hoffmann 2005; Bakker et al. 2008). However, to assess the effectiveness of seed dispersal, post-dispersal processes have to be studied (Ramos et al. 2006).

Besides its role in endozoochorous seed transport the deposition of livestock dung has further effects: gaps may be created and a local nutrient enrichment can be caused, producing favourable conditions for germination and seedling growth (Cosyns et al. 2006; Gillet et al. 2010). Furthermore, an increase of the total small-scale species diversity after dung deposition was described (Cosyns et al. 2006). The availability of seeds, microsites or both in combination may limit recruitment and establishment in plant populations (Eriksson & Ehrlén 1992; Zobel at al. 2000; Seabloom et al. 2003; Donath et al. 2007; Lindgren et al. 2007).

Trampling is a high-frequency disturbance impact on pastures (Hobbs 2006). Previous studies on trampling effects in pastures mainly focused on the gap-creating effect of hooves (e.g. Stammel & Kiehl 2004). It seemed likely that trampling also affects the germination and establishment of dung-embedded seeds, but to our knowledge this process has not been investigated so far. We hypothesised positive impacts on the post-dispersal fate of endozoochorous seeds as a consequence of cracking the dung pellets by hoof trampling. Consequently, embedded seeds come into contact with the soil, which should enhance water availability.

Hooves of ungulates not only hit plant individuals and soil substrate but also crack dung substrate of other herbivore species as was observed in our study system. In sheep-grazed systems, rabbits can develop high population densities because they

profit from the open canopy and landscape structure. Besides sheep they are important grazers with high phytomass extraction (up to 100 % regarding legumes and other herbs in the study system; Faust et al. 2007) and therefore dung deposition rates.

Our study focuses on grassland microsites where a spatial combination of the processes deposition of seed-carrying dung, nutrient enrichment and trampling exists. As a model of a threatened grazed grassland type we investigated inland sand ecosystems in a temperate region. The high phytodiversity of these systems depends on continuous disturbance dynamics (Süss et al. 2004; Eichberg et al. 2007). Extensive grazing regimes, especially those including sheep, became an important management tool in threatened grassland ecosystems and habitats with high conservation value (Bakker et al. 1983; Plassmann et al. 2010). Sheep-mediated gaps mainly exist in the form of resting places, livestock trails and hoof prints. Previous studies have shown a high endozoochorous potential of sheep and rabbits (Pakeman et al. 1999; Eichberg et al. 2007; Wessels & Schwabe 2008). In this context we tried to elucidate the fate of endozoochorously dispersed, dung-embedded seeds after they are trampled by sheep. Especially in the case of sheep an ecologically relevant effect of this link is likely, for the following reasons: first, sheep are kept in large flocks generating a high trampling density. Second, sheep scatter their dung unintentionally in special areas (e.g., resting places). Consequently the grazed area will be affected to a large extent.

We focused on the following questions: (1) Which endozoochorously dispersed plant species are contained in what quantities in sheep and rabbit dung collected from sandy grasslands? (2) What proportion of this potential is able to establish itself in the field after one or two years? (3) Are sheep trampling on dung pellets of sheep and rabbits facilitative post-dispersal processes (emergence, fruiting) for dung-embedded seeds? (4) What is the proportion of target species contained in the dung and among the emerging/fruiting seedlings?

Methods

Study sites

The investigations were conducted on two sites of inland sand ecosystems in the northern upper Rhine valley (Hesse, Germany), which were part of one large area ca. 70 years ago. Both sites are characterised by a mainly calcareous and nutrient-poor soil substrate and protected by the EU 92/43 Habitat Directive. The area “Griesheimer Düne und Eichwäldchen” (8°39’E, 49°53’N; 45 ha; hereafter “GD”) served as a source area for sheep and rabbit dung. The area “Ehemaliger August-Euler-Flugplatz von Darmstadt” (8°35’E, 49°51’N; 71 ha; “AEF”) was used for the

installation of experimental plots (sink area). The vegetation of GD is characterised by well-developed species-rich mid-successional Allio-Stipetum capillatae stands, whereas the vegetation of AEF can be classified as consolidated stages of Armerio-Festucetum trachyphyllae vegetation which are poor in species and mostly dominated by competitive grasses like *Cynodon dactylon* and *Poa angustifolia*. The topsoil of AEF mainly is slightly acidic (pH in 0.01 mol l^{-1} $CaCl_2$ ranges from 5.4 to 7.5) but in the case of disturbances, e.g. by rabbits, calcareous material is transferred to the topsoil. An extensive sheep grazing regime was newly established on both sites in the year 2000. The sheep flock (from 2002 onwards with up to 800 animals) grazed in relatively small paddocks, ca. 1 ha, for 1-9 days during summer (mainly from June to August) as long as an adequate food supply could be guaranteed. The climate is characterised by an annual precipitation of 629 mm and mean annual temperature of 11.1 °C (data from Frankfurt airport, 2000-2009, Deutscher Wetterdienst).

Dung collection

In August 2007, dung samples were taken from four tamed male Rhoen sheep, which grazed for two weeks in a 2-ha paddock in the GD area. For this purpose, dung was collected directly from the soil after defaecation. Dung from rabbits was collected in the same area and additionally max. 150 m away because rabbit dung densities were too low in the paddock to provide enough dung samples. The similarity of the adjacent vegetation and the vegetation of the paddock was proved by relevés. To allow comparability of the two dung types, only fresh pellets were collected. Pellet age was estimated by the pellets' colour, surface structure and degree of decomposition: fresh rabbit dung pellets are dark-brown and slightly glossy whereas older pellets are bleached out by the weather and wrinkled. During the sampling timeframe seeds of most species were ripe. Before grazing, all vascular plant species occurring in the paddock (presence/absence) and their phenological condition (vegetative/flowering/fruiting) were recorded. Dung was washed with tap water, dried at 40 °C in an air-circulated drying chamber and stored under dry conditions until utilisation. The washing process was needed to minimise contamination by dung-attached, non-endozoochorously dispersed seeds whereas the drying process was needed to define weight of dung as reference quantity.

Experiment in climate room

To test the potential seed availability of dung samples we used the Ter Heerdt method for sampling concentration (Ter Heerdt et al. 1996) which had been adapted for dung samples by Wessels & Schwabe (2008). In total, 1920 g (dry weight) crumbled and concentrated sheep dung (D_S) was divided into 48 samples of 40 g dry weight each. Exactly the same was done with the rabbit dung samples (D_R). All trays

were established in a climate room with a day/night air temperature of 20/5 °C and 16 h light (PPFD 300-800 μmol $m^{-2}s^{-1}$) per day. Water was provided daily up to field capacity. To protect the samples against Nematocera, the larvae of which colonise dung and feed on fungus hypha and young plant roots, we used yellow sticky plates. The samples were exposed for a 16-week-period: two 6-wk intervals of exposure in the climate room were interrupted by a 4-wk interval of stratification in a dark cold house (air temperature 0-4 °C). Seedling emergence was recorded throughout with the help of determination literature (Hanf 1999; Muller 1978). Identified seedlings were removed; unidentified plants were transplanted to bigger pots until determination was possible.

Field experiment

Experimental design

In the beginning of November 2007, we started a 2-year factorial field experiment in consolidated Armerio-Festucetum trachyphyllae vegetation. Three sheep + rabbit exclosures - established in 1999 - were used as an experimental area. In 2007, they were additionally protected against rabbits with fine chicken-wire netting. Within each exclosure two 5 m x 5 m plots were established, one for preliminary vegetation analyses (which showed a high degree of similarity of the three exclosures) and another one for the establishment of plots for the trampling experiment.

The following two factors were investigated: dung (D_0, control; D_S, sheep; D_R, rabbit) and trampling (T_0, control; T_1, trampling). Thus, six treatments (D_0T_0 / D_0T_1 / D_ST_0 / D_ST_1 / D_RT_0 / D_RT_1) were applied, eight-fold replicated in each case, and randomly distributed within the plot area in the three exclosures (completely randomised block design). In total, 144 plots were established. Plot size was 15 cm x 15 cm according to Eichberg et al. (2007). Before application of dung and/or trampling, the soil surface of each plot was experimentally disturbed by spades and

Figure 4.1: Experimental plots with disturbance as pre-treatment and sheep-dung treatment afterwards (left side: without trampling; right side: with trampling).

hand rakes. This pre-treatment of every plot was carried out to simulate disturbed areas which are more likely to be colonised by new plant individuals (Bullock et al. 2002; Cosyns et al. 2006). We carefully removed the complete above-ground vegetation and as much below-ground plant material as possible without losing too much soil. The total disturbed area of each plot was 25 cm x 25 cm (Eichberg et al. 2007). Plot-surrounding vegetation was clipped in spring and autumn. On each dung plot, 40 g dung pellets were distributed as a closed single-layer (in total 1920 g dung dry weight per dung type; Fig. 4.1).

Experimental trampling was done with replicas of sheep hooves (Fig. 4.2). For that purpose we used 12 hoof replicas, which were screwed on a wooden cube to obtain a trampling stamp of approximately plot size. Dung was trampled in a manner of stamping as long as it took to crack every pellet (Fig. 4.1, right side). Plots without dung but with trampling treatment were trampled with the same intensity. Hooves were cleaned thoroughly between the trampling procedures to avoid any dung transfer between plots.

Figure 4.2: Trampling stamp with sheep-hoove replicas.

To prevent disturbance by dung beetles, especially dung predation by *Typhaeus typhoeus* (Geotrupidae), we protected every plot aboveground with a fine wire cage (mesh size: 6 mm x 6 mm) and belowground with a plastic lawn border which was dug 25 cm into the soil additionally. Cages were only used from autumn till spring, when dung beetles had their active life-cycle periods.

Vegetation sampling

On each plot, all soil- and dung-borne plant individuals and vegetative sprouts were recorded in spring and autumn (by far the main germination periods in the dry study system) in each of the two study years 2008 and 2009 as presence-absence data (hereafter "Field data set A"). We studied two years to analyse plant species with different life cycles like biennials, which flower only in the second year, or annuals, which may not germinate in the first but in the second year of the study. In addition, dung-borne seedlings were counted (hereafter "Field data set B"). Seedlings that emerged and died within the periods between counts could not be

recorded, but germination events between the counts are relatively rare. During recordings the current condition (vegetative/flowering/fruiting) of every dung-borne seedling was assessed. For a correct detection as "dung-borne" we had to observe the origin of the seedlings very carefully. This could be done quite easily on plots without trampling treatment because dung-borne seedlings rooted in the uncracked pellets. On plots with trampling treatment we had to examine whether seedlings rooted in the dung layer of the cracked and clumped pellets or if the seedlings originated from the soil substrate beneath. To follow the individual fate of dung-borne seedlings we marked them with small sticks.

The data of both study years were pooled within both data sets. Nomenclature follows Wisskirchen & Haeupler (1998). *Chenopodium album* and *C. strictum* were pooled for both field data sets.

Data analysis

The qualitative (TSR_{qual}) and quantitative ratio of target species (TSR_{quant}; Eichberg et al. 2010) was calculated to elucidate whether target species are facilitated due to endozoochory and trampling or not. Target species are considered as species with main occurrence in the classes Festuco-Brometea, 'steppes, rocky steppes and sandy grasslands of the sub-continental temperate and sub-boreal regions', or Koelerio-Corynephoretea, 'pioneer vegetation on primitive soils and rocky outcrops in regions with mild winter climate' (according to ETC/BD 2008). TSR ratios were calculated by the following formulas:
TSR_{qual} = number of target plant species/total number of plant species;
TSR_{quant} = sum of target plant individuals/total sum of plant individuals.

The following data were analysed by mixed linear models (SAS 9.2, PROC GLIMMIX, SAS Institute Inc., Cary, NC, USA; Littell et al. 2006): 1. Climate room data (D_S/D_R), 2. Field data set A (D_0T_0 / D_0T_1 / D_ST_0 / D_ST_1 / D_RT_0 / D_RT_1), 3. Field data set B (D_ST_0 / D_ST_1 / D_RT_0 / D_RT_1). For the latter two models, the exclosure (block) was included as random effect. The influence on the following dependent variables was assessed: number of emerging species, number of emerging seedlings, number of fruiting individuals, both TSR indices and all single species. For both field data sets Tukey-adjusted post hoc tests were carried out to test for effects of treatments (using the 'slice' option of PROC GLIMMIX).

For the calculation of degrees of freedom, we selected the Kenward-Roger approximation as recommended by Schaalje et al. (2001, 2002) and Arnau et al. (2009). Vallejo et al. (2004) and Jacqmin-Gadda et al. (2007) were able to show that mixed linear models using this method are robust against deviation from normal distributions both in terms of error control and power. Nevertheless, the studentised residuals and conditional studentised residuals were examined for normality by

means of graphical display (histograms and quantile-residuum plots); a nearly Gaussian distribution could be ascertained.

Results

Species pool of the actual vegetation of the source area (Table 1)

In total, 59 vascular plant taxa were present on the experimental sheep paddock (source area), 37 of which were in fruiting condition (17 target species, 20 non-target species). The qualitative ratio of target species (TSR_{qual}) which set fruits in the paddock was 0.46. Among the fruiting species most were short-lived: 18 annuals (49 %), 5 biennials (13 %) and 14 perennials (38 %).

Climate room data (Tables 4.1, 4.2)

In sheep dung we found 26 species and 100.5 ± 8.2 seedlings (± 95 % confidence interval, CI) per 100 g air-dry dung, in rabbit dung 31 species and 85.9 ± 8.6 seedlings per 100 g air-dry dung emerging after the 18-week experiment. As shown in the Tables the spectra of endozoochorously dispersed species from sheep and rabbit dung were to a higher degree complementary than concordant. Differences regarding the numbers of species and seedlings were significant. Nine species showed a significantly higher seed content in sheep than rabbit dung; among them the three dominant species were tall-growing (> 50 cm): *Oenothera biennis* s.l. (66 % of the seedlings; 66.2 ± 6.5 seedlings per 100 g), *Verbascum phlomoides* and *Amaranthus retroflexus*. Eight species were significantly more abundant in rabbit than in sheep dung, all of which were small- and medium-growing species (≤ 50 cm): e.g. *Agrostis capillaris* (42 % of the seedlings; 36.3 ± 5.7 seedlings per 100 g), *Fragaria* x *ananassa* and *Arenaria serpyllifolia* agg. Short-lived species represented the dominant life form in both dung types: a) sheep dung 58 % annuals, 12 % biennials and 30 % perennials, b) rabbit dung 61 % annuals, 13 % biennials and 26 % perennials. Furthermore, predominantly small-seeded species (size groups 1 or 2) were found in both dung types.

Next page:

Table 4.1: Synoptic table showing all single plant species and fates across the different stages of generative regeneration including fruiting in the actual vegetation, endozoochorous seed dispersal and establishment. G = species group (t: target, n: non-target); L = life cycle (a: annual, b: biennial, p: perennial); H = growth height (based upon observations in the field: 1: < 20 cm, 2: 20-50 cm, 3: > 50 cm, w: woody species); S = seed size group (1: < 1.0 mm, 2: 1.0-2.0 mm, 3: 2.1-3.0 mm, 4: 3.1-4.0 mm, 5: > 4.0 mm). Data on L and S according to Klotz, Kühn & Durka (2002). ○ = species occurred in one plot/sample only; ● = frequency of occurrence in plots/samples < 5 %; ●● = frequency of occurrence in plots/samples 5-50 %; ●●● = frequency of occurrence in plots/samples > 50 %; + = species was present on the studied sheep paddock in fruiting condition.

					seed potential (climate room)		establishment (field experiment)								actual vegetation (sheep paddock)
							seedling emergence				fruiting success				
	G	L	H	S	D_S	D_R	D_ST_0	D_ST_1	D_RT_0	D_RT_1	D_ST_0	D_ST_1	D_RT_0	D_RT_1	fruiting species
Present in sheep and rabbit dung, successful emergence and fruiting															
Oenothera biennis s.l.	n	b	3	2	●●●	●●●	●●●	●●●	●●	●●●	●●	●●		●●	+
Potentilla argentea agg.	t	p	1	1	●●●	●●●	●	●●	●●	●●		●●	●●	●	+
Arenaria serpyllifolia agg.	t	a	1	1	●●	●●●	●●	●●	●●	●●	●●	●●	○	●●	+
Verbascum phlomoides	n	b	3	1	●●●	●●	●●	●●	●●	●●		●●	●●	●●	+
Conyza canadensis	n	a	2	2	●●	●●	●●	●●	●●	●●	○	●	●●	●●	+
Sedum acre	t	p	1	1	●●	●●		●●	●●	●●		○	○	●●	+
Vicia lathyroides	t	a	1	2	○	●		●●	●●	●●		○	○	●●	
Only present in sheep dung, successful emergence and fruiting															
Chenopodium album agg.	n	a	2	2	●●		●●	●●	●	●●		○	○	○	
Trifolium campestre	t	a	1	2	●					●●				○	+
Only present in rabbit dung, successful emergence and fruiting															
Rumex acetosella s.l.	t	a	1	2		●●●		●		●●				●	
Alyssum alyssoides	t	a	1	2		●●			●●	○				○	+
Cerastium semidecandrum	t	a	1	1		●●				○				○	
Petrorhagia prolifera	t	a	2	2		●●				●●				○	+
Centaurea stoebe s.l.	t	b	3	3		○			○				○		+
Erodium cicutarium agg.	t	a	1	3		○				○				○	+
Present in either sheep or rabbit dung, successful emergence															
Poa angustifolia	n	p	2	2	●				○						
Crepis capillaris	n	a	2	3		○				○					+
Present in sheep and rabbit dung, no establishment															
Fragaria x *ananassa*	n	a	1	2	○	●●●									
Echium vulgare	t	b	2	3	●●	●●									+
Portulaca oleracea	n	a	1	1	●●	●●									+
Urtica dioica s.l.	n	p	3	2	●●	●●									
Solanum nigrum	n	a	2	2	●	●●									+
Psyllium arenarium	n	a	1	3	●	●									+
Medicago minima	t	a	1	2	●	○									+
Robinia pseudoacacia	n	p	w	5	○	○									
Only present in sheep dung, no establishment															
Amaranthus retroflexus	n	a	3	2	●●●										+
Chenopodium strictum	n	a	2	2	●●●										
Diplotaxis tenuifolia	n	p	2	2	●●										+
Herniaria glabra	t	a	1	1	●●										
Saponaria officinalis	n	p	3	2	●●										
Cynodon dactylon	n	p	2	1	●										
Geranium molle	n	a	1	2	○										+
Myosotis ramosissima	t	a	1	2	○										
Only present in rabbit dung, no establishment															
Agrostis capillaris	n	p	2	1		●●●									
Veronica praecox	t	a	1	2		●●									
Silene conica	t	a	1	1		●									
Spergula arvensis	n	a	2	2		●									
Thymus pulegioides	n	p	1	1		●									
Agrostis vinealis	t	p	2	2		○									
Eragrostis minor	n	a	1	1		○									
Koeleria macrantha	t	p	2	3		○									
Stellaria media	n	a	1	2		○									
Neither found in sheep nor rabbit dung, successful seedling emergence															
Helianthemum nummularium ssp. *obscurum*	t	p	1	2			●●	●●							+
Veronica arvensis	n	a	1	1					●●						
Vicia angustifolia	t	a	1	2					●				○		
Silene otites	t	p	3	1						○					
Only present in the actual vegetation															
Achillea millefolium	n	p	2	2											+
Agrimonia procera	n	p	3	5											+
Berteroa incana	n	a	2	2											+
Carduus nutans	n	b	3	4											+
Corynephorus canescens	t	p	1	1											+
Helichrysum arenarium	t	p	2	1											+
Hypericum perforatum	n	p	3	2											+
Medicago falcata (incl. *M.* x *varia*)	t	p	2	3											+
Ononis repens	t	p	1	3											+
Pinus sylvestris	n	p	w	5											+
Rumex obtusifolius	n	p	3	3											+
Salsola kali ssp. *tragus*	n	a	2	2											+
Setaria viridis	n	a	1	3											+
Sisymbrium altissimum	n	a	3	1											+
Stipa capillata	t	p	3	5											+
Veronica verna	t	a	1	1											+
Total number of species:					26	31	7	10	13	16	3	8	9	14	37

Table 4.2: Climate room data. Mean content of viable seeds per 100 g air-dried faeces (with ± 95 % confidence interval, CI, in parentheses) and the results of the SAS mixed-linear-model analysis of significant influences of the dung type. No. of samples of each dung type: 48; total dry weight of faeces of each dung type: 1920 g. Fr: frequency of occurrence in samples (%). Num df: degrees of freedom Numerator, Den df: degrees of freedom Denominator, p: level of significance.

Species	Sheep dung	Fr	Rabbit dung	Fr	Num df	Den df	F value	p
Significantly higher content in sheep dung								
Amaranthus retroflexus	5.21 (1.33)	79	0	0	1	94	59.10	<0.0001
Chenopodium album	1.25 (0.65)	33	0	0	1	94	14.10	0.0003
Chenopodium strictum	2.34 (0.57)	67	0	0	1	94	64.35	<0.0001
Echium vulgare	0.68 (0.43)	21	0.16 (0.17)	6	1	94	4.83	0.0305
Herniaria glabra	0.36 (0.25)	15	0	0	1	94	8.02	0.0056
Oenothera biennis s.l.	66.20 (6.47)	100	13.80 (1.91)	100	1	94	231.75	<0.0001
Portulaca oleracea	1.46 (0.56)	44	0.16 (0.17)	6	1	94	18.84	<0.0001
Sedum acre	1.61 (0.64)	44	0.52 (0.29)	21	1	94	9.21	0.0031
Verbascum phlomoides	12.08 (1.91)	100	2.76 (0.56)	42	1	94	110.47	<0.0001
Significantly higher content in rabbit dung								
Agrostis capillaris	0	0	36.25 (5.71)	98	1	94	109.20	<0.0001
Alyssum alyssoides	0	0	0.73 (0.36)	27	1	94	16.10	0.0001
Arenaria serpyllifolia agg.	2.08 (0.87)	46	5.36 (1.29)	83	1	94	17.15	<0.0001
Cerastium semidecandrum	0	0	0.73 (0.38)	25	1	94	13.79	0.0003
Conyza canadensis	0.21 (0.20)	8	0.89 (0.40)	31	1	94	8.87	0.0037
Fragaria x *ananassa*	0.16 (0.31)	2	11.56 (3.13)	85	1	94	50.38	<0.0001
Rumex acetosella s.l.	0	0	3.23 (0.95)	65	1	94	44.85	<0.0001
Solanum nigrum	0.10 (0.14)	4	1.46 (0.94)	31	1	94	7.73	0.0065
No significant differences								
Agrostis vinealis	0	0	0.05 (0.10)	2	1	94	1.00	0.3199
Centaurea stoebe s.l.	0	0	0.05 (0.10)	2	1	94	1.00	0.3199
Crepis capillaris	0	0	0.05 (0.10)	2	1	94	1.00	0.3199
Cynodon dactylon	0.10 (0.14)	4	0	0	1	94	2.04	0.1562
Diplotaxis tenuifolia	0.16 (0.17)	6	0	0	1	94	3.13	0.0799
Eragrostis minor	0	0	0.05 (0.10)	2	1	94	1.00	0.3199
Erodium cicutarium agg.	0	0	0.05 (0.10)	2	1	94	1.00	0.3199
Geranium molle	0.05 (0.10)	2	0	0	1	94	1.00	0.3199
Koeleria macrantha	0	0	0.05 (0.10)	2	1	94	1.00	0.3199
Medicago minima	0.10 (0.20)	2	0.05 (0.10)	2	1	94	0.20	0.6557
Myosotis ramosissima	0.05 (0.10)	2	0	0	1	94	1.00	0.3199
Petrorhagia prolifera	0	0	0.16 (0.17)	6	1	94	3.13	0.0799
Poa angustifolia	0.10 (0.14)	4	0	0	1	94	2.04	0.1562
Potentilla argentea agg.	5.47 (1.14)	90	7.40 (1.62)	90	1	94	3.65	0.0591
Psyllium arenarium	0.10 (0.14)	4	0.10 (0.14)	4	1	94	0.00	1.000
Robinia pseudoacacia	0.05 (0.10)	2	0.05 (0.10)	2	1	94	0.00	1.000
Saponaria officinalis	0.16 (0.17)	6	0	0	1	94	3.13	0.0799
Silene conica	0	0	0.10 (0.14)	4	1	94	2.04	0.1562
Spergula arvensis	0	0	0.10 (0.14)	4	1	94	2.04	0.1562
Stellaria media	0	0	0.05 (0.10)	2	1	94	1.00	0.3199
Thymus pulegioides	0	0	0.10 (0.14)	4	1	94	2.04	0.1562
Trifolium campestre	0.10 (0.14)	4	0	0	1	94	2.04	0.1562
Urtica dioica s.l.	0.26 (0.33)	6	0.94 (0.88)	17	1	94	1.98	0.1631
Veronica praecox	0	0	0.16 (0.17)	6	1	94	3.13	0.0799
Vicia lathyroides	0.05 (0.10)	2	0.10 (0.14)	4	1	94	0.34	0.5623
Total no. of species	26		31					
Mean no. of seeds per 100 g	100.52 (8.22)		85.88 (8.63)		1	94	102.20	<0.0001
Mean TSR_{qual}	0.31 (0.04)		0.32 (0.03)		1	94	0.11	0.7373
Mean TSR_{quant}	0.10 (0.02)		0.13 (0.02)		1	94	6.91	0.0100

The TSR_{qual} regarding the total number of species was 0.38 for sheep dung and 0.52 for rabbit dung, whereas the mean TSR_{qual} was in both dung types nearly identical: 0.31 ± 0.04 (sheep dung) and 0.32 ± 0.03 (rabbit dung). Regarding the TSR_{quant} rabbit dung samples showed slightly higher values (0.13 ± 0.02) than sheep dung samples (0.10 ± 0.02). Only differences in dung type regarding TSR_{quant} were significant.

With reference to the species pool of the sampled sheep paddock we found 50 % (9 species) of the fruiting annual species in sheep dung again (biennials: 60 %, 3 species), in the case of rabbit dung 56 % (10 species; biennials: 80 %, 4 species). The percentages of fruiting perennials were 60 % (3 species, sheep dung) or 14 % (2 species, rabbit dung). Five species emerged from sheep dung and 12 species from rabbit dung samples, which were neither recorded in fruiting nor in vegetative condition in the paddock.

Field experiment

Field data set A (dung- and soil-borne individuals, Tab. 4.3)

Species numbers (mean ± 95 % CI) were lowest on plots without dung (D_0T_0: 5.17 ± 0.71; D_0T_1: 5.25 ± 0.58) and highest on plots with a combination of dung and trampling treatment (D_ST_1: 7.13 ± 0.56; D_RT_1: 7.38 ± 0.62). Species numbers on D_ST_0 plots were only slightly higher than on plots without dung; plots with rabbit dung but without trampling (D_RT_0) showed 6.42 ± 0.86 species. Statistical analyses revealed a significant positive impact of dung as well as trampling on the species number. No significant interaction dung*trampling occurred, but, by trend, the data show a more pronounced trampling effect on sheep dung than on rabbit dung and a negligible effect on plots without dung.

Table 4.3: Field data set A. Mean number of species (presence-absence data; with ± 95 % confidence interval, CI, in parentheses) per plot (No. of plots per treatment: 24; plot size: 225 cm²) and the results of the SAS mixed-linear-model analysis of influences of the independent variables dung and trampling and/or interaction effects. Means sharing the same letter are not significantly different (p>0.05). Num df: degrees of freedom Numerator, Den df: degrees of freedom Denominator, p: level of significance.

treatment	No. of species
D_0T_0	5.17^{a} (0.71)
D_0T_1	5.25^{a} (0.58)
D_ST_0	5.67^{ab} (0.68)
D_ST_1	7.13^{c} (0.56)
D_RT_0	6.42^{bc} (0.86)
D_RT_1	7.38^{c} (0.62)

effect	Num df	Den df	F value	p
dung	2	138	12.59	<0.0001
trampling	1	138	8.73	0.0037
dung*trampling	2	138	2.03	0.1353

Field data set B (dung-borne individuals)

Emergence success (Tab. 4.1, 4.4, 4.5)

Again, the interaction of dung*trampling exerted no significant influence on any tested variable; hence the two main effects can be analyzed separately.

The effect of dung type was less pronounced than in the climate room data. The mean numbers of species and seedlings were only slightly and insignificantly higher in rabbit dung. Only *Oenothera biennis* s.l. and *Helianthemum nummularium* ssp. *obscurum* emerged in significantly higher numbers or exclusively from sheep dung. Dung type exerted significant effects on both TSR indices, with higher values in rabbit dung.

The effect of trampling, however, was considerable and increased the mean number of species and seedlings significantly: The sheep dung plots with trampling treatment showed a 3.6-fold higher seedling emergence than plots without. In addition, the mean number of species was 2.4-fold higher with trampling on sheep dung. In the case of rabbit dung, the seedling emergence was 2.1-fold higher with trampling treatment and the mean number of species was 1.9-fold higher.

Significant effects of trampling occurred for the species *Arenaria serpyllifolia* agg. (increase by factor 3.5 on sheep dung and 9.4 on rabbit dung) and *Oenothera biennis* s.l. (factors 3.5 and 6.4). Trampling of sheep dung slightly favoured eight further species and none was suppressed. The favoured species are 50 % annuals, 20 % biennials and 30 % perennials; altogether 80 % are small- or medium-growing species. In the case of rabbit dung, 10 further species benefited and 7 were impaired, but most of them lost only 4 % in frequency which equals one plot. Regarding their life cycles, mainly short-lived species benefited from trampling on rabbit dung (83 % annuals, 8 % biennials). Again, the highest percentages were small- or medium-growers (83 %). A high amount of seedlings, e.g., of *Arenaria serpyllifolia* agg., *Conyza canadensis* or *Potentilla argentea* agg., were recorded in spring of the second study year. *Chenopodium album/strictum* was the only taxon which germinated, flowered and fruited only in the first year.

The emergence success of sheep dung-borne seedlings in the field was only 5 % without trampling, or 18 % with trampling, of the potential in the climate room; the success on rabbit dung plots was similar: 7 % of the potential without trampling or 14 % with trampling treatment. As found for the climate room data, the emergence success was highest for small-seeded species. We found eight species which emerged from dung samples in the climate room but not in the field experiment.

	Num df	Den df	No. of seedlings		No. of species		TSR_{qual}		TSR_{quant}		*Arenaria serpyllifolia* agg.		*Helianthemum nummularium* ssp. *obscurum*		*Oenothera biennis* s.l.	
			F value	p	F value	p	F value	p	F value	p	F value	p	F value	p	F value	p
A. Seedling emergence																
dung	1	92	0.45	0.5028	0.07	0.7980	**4.48**	**0.0371**	**6.68**	**0.0114**	2.06	0.1547	**4.95**	**0.0285**	**5.88**	**0.0172**
trampling	1	92	**21.14**	**<0.0001**	**22.86**	**<0.0001**	**5.73**	**0.0187**	2.92	0.0911	**5.46**	**0.0216**	0.42	0.5170	**13.00**	**0.0005**
dung*trampling	1	92	1.08	0.3009	0.53	0.4668	0.18	0.6762	0.00	0.9606	1.71	0.1937	0.42	0.5170	0.47	0.4934
B. Fruiting success																
dung	1	92	0.01	0.9409	1.29	0.2588	**6.71**	**0.0212**	**7.84**	**0.0062**	0.35	0.5534	-	-	**9.44**	**0.0028**
trampling	1	92	**14.38**	**0.0003**	**8.43**	**0.0046**	2.07	0.1537	2.18	0.1431	1.93	0.1685	-	-	**7.72**	**0.0066**
dung*trampling	1	92	0.27	0.6039	0.02	0.8998	0.33	0.5664	0.62	0.4336	0.98	0.3241	-	-	1.05	0.3086

Table 4.4: Field data set B. Results of the SAS mixed-linear-model analysis of significant influences of the independent variables dung and trampling and/or interaction effects on (A) the number of seedlings emerging and (B) the number of individuals fruiting. Significant effects are shown in bold print. Num df: degrees of freedom Numerator, Den df: degrees of freedom Denominator, p: level of significance. A dash indicates that no test was done, because no individuals fruited successfully. The following species were tested but did not reveal significant results: *Alyssum alyssoides*, *Centaurea stoebe* s.l., *Cerastium semidecandrum*, *Chenopodium album* agg., *Conyza canadensis*, *Crepis capillaris*, *Erodium cicutarium* agg., *Petrorhagia prolifera*, *Poa angustifolia*, *Potentilla argentea* agg., *Rumex acetosella* s.l. , *Sedum acre*, *Silene otites*, *Trifolium campestre*, *Verbascum phlomoides*, *Veronica arvensis*, *Vicia angustifolia*, *Vicia lathyroides*.

Besides, *Helianthemum nummularium* ssp. *obscurum* was found in sheep dung in the field experiment but did not emerge in the climate room. *Arenaria serpyllifolia* agg. and *Verbascum phlomoides* showed a high seed content in sheep dung samples in the climate room but in the field experiment seedlings of *Arenaria* predominantly emerged from rabbit dung whereas seedlings of *V. phlomoides* emerged in higher abundances from both dung types. The high number of *Oenothera biennis* s.l. seedlings from sheep dung or *Conyza canadensis* seedlings from rabbit dung samples in the climate room corresponds to the high number of seedlings of these species in the field. In total, 24 species did not emerge from dung samples in the field experiment, most of which (16) had very low numbers of emerged individuals in the climate room.

Next page:
Table 4.5: Field data set B. Mean number of emerging seedlings (A) and fruiting individuals (B) per 100 g air-dry faeces (with ± 95 % confidence interval, CI, in parentheses) within 2 years. No. of plots of each treatment type: 24; total dry weight of faeces of each plot type: 960 g. Fr: frequency of occurrence in plots (%). Means sharing the same letter are not significantly different (p>0.05).

Plot type	D_ST_0		Fr	D_ST_1		Fr	D_RT_0		Fr	D_RT_1		Fr
A. Seedling emergence												
Alyssum alyssoides	0		0	0		0	0.52	(0.83)	8	0.10	(0.20)	4
Arenaria serpyllifolia agg.	0.21 [a]	(0.28)	8	0.73 [a]	(0.81)	13	0.21 [ab]	(0.28)	8	1.98 [b]	(1.22)	38
Centaurea stoebe s.l.	0		0	0		0	0.10	(0.20)	4	0		0
Cerastium semidecandrum	0		0	0		0	0		0	0.10	(0.20)	4
Chenopodium album agg.	0.21	(0.28)	8	0.73	(0.62)	21	0.21	(0.41)	4	0.31	(0.45)	8
Conyza canadensis	0.31 [a]	(0.45)	8	0.94 [ab]	(1.01)	17	0.52 [ab]	(0.59)	13	1.98 [b]	(1.50)	33
Crepis capillaris	0		0	0		0	0		0	0.10	(0.20)	4
Erodium cicutarium agg.	0		0	0		0	0		0	0.10	(0.20)	4
Helianthemum nummularium s.l.	0.42	(0.48)	13	0.83	(0.76)	21	0		0	0		0
Oenothera biennis s.l.	2.71 [a]	(1.06)	58	9.48 [b]	(2.96)	92	0.52 [a]	(0.59)	13	3.33 [a]	(1.46)	67
Petrorhagia prolifera	0		0	0		0	0		0	0.21	(0.28)	8
Poa angustifolia	0		0	0		0	0.10	(0.20)	4	0		0
Potentilla argentea agg.	0.73 [a]	(1.43)	4	2.81 [b]	(2.01)	42	1.46 [ab]	(1.02)	29	1.25 [ab]	(0.78)	33
Rumex acetosella s.l.	0		0	0.42	(0.82)	4	0		0	0.83	(1.13)	8
Sedum acre	0		0	0.52	(0.51)	17	0.21	(0.28)	8	0.31	(0.45)	8
Silene otites	0		0	0		0	0		0	0.10	(0.20)	4
Trifolium campestre	0		0	0		0	0		0	0.21	(0.28)	8
Verbascum phlomoides	0.42	(0.48)	13	1.46	(0.97)	38	1.46	(1.02)	33	0.73	(0.69)	17
Veronica arvensis	0		0	0		0	0.21	(0.28)	8	0		0
Vicia angustifolia	0		0	0		0	0.21	(0.41)	4	0		0
Vicia lathyroides	0		0	0.21	(0.28)	8	0.21	(0.28)	8	0.63	(0.53)	21
Number of species per plot type	7			10			13			16		
Mean no. of seedlings per 100 g	5.00 [a]	(2.13)		18.13 [c]	(5.63)		5.94 [ab]	(1.97)		12.29 [b]	(3.18)	
Mean no. of species per treatment	1.13 [a]	(0.36)		2.71 [c]	(0.51)		1.46 [ab]	(0.44)		2.71 [bc]	(0.63)	
Mean TSR_{qual}	0.16 [a]	(0.13)		0.35 [b]	(0.10)		0.33 [ab]	(0.17)		0.46 [b]	(0.13)	
Mean TSR_{quant}	0.16 [a]	(0.13)		0.27 [ab]	(0.08)		0.33 [ab]	(0.17)		0.45 [b]	(0.13)	
B. Fruiting success												
Alyssum alyssoides	0		0	0		0	0		0	0.10	(0.20)	4
Arenaria serpyllifolia agg.	0.21	(0.28)	8	0.31	(0.45)	8	0.10	(0.20)	4	0.73	(0.86)	13
Centaurea stoebe s.l.	0		0	0		0	0.10	(0.20)	4	0		0
Cerastium semidecandrum	0		0	0		0	0		0	0.10	(0.20)	4
Chenopodium album agg.	0		0	0.10	(0.20)	4	0.10	(0.20)	4	0.10	(0.20)	4
Conyza canadensis	0.10	(0.20)	4	0.21	(0.41)	4	0.21	(0.28)	8	0.52	(0.51)	17
Crepis capillaris	0		0	0		0	0		0	0		0
Erodium cicutarium agg.	0		0	0		0	0		0	0.10	0.20	4
Helianthemum nummularium s.l.	0		0	0		0	0		0	0		0
Oenothera biennis s.l.	0.73 [a]	(0.46)	29	2.08 [b]	(1.20)	38	0		0	0.63 [a]	(0.53)	21
Petrorhagia prolifera	0		0	0		0	0		0	0.10	0.20	4
Poa angustifolia	0		0	0		0	0		0	0		0
Potentilla argentea agg.	0		0	0.63	(0.90)	8	0.21	(0.28)	8	0.21	0.41	4
Rumex acetosella s.l.	0		0	0		0	0		0	0.31	0.61	4
Sedum acre	0		0	0.10	(0.20)	4	0.10	(0.20)	4	0.21	(0.28)	8
Silene otites	0		0	0		0	0		0	0		0
Trifolium campestre	0		0	0		0	0		0	0.10	0.20	4
Verbascum phlomoides	0		0	0.52	(0.51)	17	0.42	(0.38)	17	0.31	(0.34)	13
Veronica arvensis	0		0	0		0	0		0	0		0
Vicia angustifolia	0		0	0		0	0.10	(0.20)	4	0		0
Vicia lathyroides	0		0	0.10	(0.20)	4	0.10	(0.20)	4	0.31	(0.45)	8
Number of fruiting species per plot type	3			8			9			14		
Mean no. of fruiting individuals per 100 g	1.04 [a]	(0.50)		4.06 [c]	(1.93)		1.46 [ab]	(0.72)		3.85 [bc]	(1.67)	
Mean no. of fruiting species per treatment	0.42 [a]	(0.20)		0.88 [ab]	(0.85)		0.58 [ab]	(0.29)		1.08 [b]	(0.42)	
Mean TSR_{qual}	0.08 [a]	(0.11)		0.15 [a]	(0.13)		0.23 [ab]	(0.16)		0.38 [b]	(0.17)	
Mean TSR_{quant}	0.08 [a]	(0.11)		0.13 [a]	(0.12)		0.23 [ab]	(0.16)		0.39 [b]	(0.17)	

Fruiting success (Tab. 4.1, 4.4, 4.5)

The fruiting success was not significantly influenced by dung type but increased by trampling treatment. Hence, the number of fruiting seedlings as well as the number of fruiting species was higher on plots with trampling on dung. Regarding plots with sheep dung, the number of fruiting individuals per 100 g dung was 3.9-fold higher with trampling and the number of fruiting species was 2.1-fold higher. In case of rabbit dung, the number of fruiting individuals was 2.6-fold higher and the number of fruiting species 1.9-fold higher. If separated into the plot types, 21 % of the seedlings on D_ST_0 plots had fruiting success, 22 % on D_ST_1 plots, 25 % on D_RT_0 plots and on D_RT_1 plots 31 % of the emerged seedlings were able to set seeds. In general, the percentage of short-lived species which fruited successfully was very high (range of the former treatment combinations: 75-100 %) as well as the percentage of small- or medium-growing species (66-85 %).

With one exception, the fruiting success of single plant species was not significantly affected by treatments: *Oenothera biennis* s.l. was significantly influenced by dung as well as trampling treatment.

Target species ratio (TSR; Tab. 4.4, 4.5)

In case of the total TSR_{qual} the seedling emergence values were 1.4-fold higher on sheep dung plots with trampling treatment; values on plots with rabbit dung were about 1.3-fold higher with trampling. Trampling exerted in case of the total TSR_{quant} only minor differences within one dung type, whereas values on rabbit dung plots were generally 1.6- or 1.8-fold higher than on sheep dung plots. Regarding the fruiting success, there were no differences due to trampling on rabbit dung plots in case of the total TSR_{qual}, but on sheep dung plots with trampling the fruiting success of target species was 1.5-fold higher. Again, trampling enhanced the quantitative fruiting success of target individuals (TSR_{quant}) on both dung types slightly (1.4- or 1.2-fold).

The effects of trampling as well as dung types significantly influenced the mean TSR_{qual} regarding the seedling emergence. Hence, target species benefited from both factors. The effect of trampling was more pronounced on plots with sheep dung and therefore, the emergence of target species was 2.2-fold higher with trampling; on rabbit dung plots values were only 1.4-fold higher. Also the fruiting success of target species was enhanced by trampling but in this case insignificantly: values were 1.9- or 1.7-fold higher and only the dung type exerted significant results. Trampling did not affect the emergence or fruiting success of target individuals significantly (TSR_{quant}) but differences in dung type were significant. Anyhow, values of TSR_{quant} regarding the seedling emergence were 1.7- or 1.4-fold higher with trampling and regarding the fruiting success values were 1.6- or 1.7-fold higher.

Discussion

Seed availability (climate room experiment; question 1)

The seed density found in sheep dung which was sampled from the reference area with Allio-Stipetum vegetation (101 seeds 100 g^{-1} air-dry dung) is similar to the results of Mouissie (2004: 105 seeds 100 g^{-1} air-dry dung) in a Dutch heathland-grassland-woodland mosaic, higher than in a study by Kuiters & Huiskes (2010: 80 seeds 100 g^{-1} dry matter) in Dutch calcareous grassland and lower than in the experiment by Eichberg et al. (2007: 124 seeds 100 g^{-1} air-dry dung) in sandy Koelerion glaucae vegetation. Furthermore, the number of taxa (26) found in sheep faeces is similar to the results of Eichberg et al. (2007; 28 taxa) and Mitlacher et al. (2002; 27) but much lower than in the study by Kuiters & Huiskes (2010; 72). Concerning the number of seeds and taxa in rabbit dung (86 seeds 100 g^{-1} air-dry dung) the results have shown that our dung samples had a diaspore content only half as large as in experiments conducted by Jährling (unpublished data; 166 seeds 100 g^{-1} air-dry dung) in the same area. The number of taxa (31) was quite similar to those found by Jährling (unpubl. data; 37 taxa).

With high probability, the differences in diaspore density and number of species between sheep and rabbit dung are caused by different dietary preferences of the two herbivores. Sheep ate more tall-growing species like *Oenothera biennis* s.l. or *Verbascum phlomoides*, whereas rabbit dung contained seeds of many small- or medium-growing species which were predominantly annuals, e.g. *Arenaria serpyllifolia* agg., *Silene conica*, *Petrorhagia prolifera*, *Vicia lathyroides*, *Thymus pulegiodes* or *Eragrostis minor*. Since many target species are small, the home range size of rabbits varies based on population densities and quality of food supply (Myers & Poole 1963). We suppose that this is also an explanation regarding those species which were found in dung samples but not on the paddock. For example, the abundance of *Fragaria* x *ananassa* seeds in rabbit dung was very high. Strawberries were cultivated on arable fields adjacent to the sampling area. In the case of sheep we assume that sheep may have eaten seed-containing plant or soil material from the litter layer.

Establishment success in the field (question 2)

Differences between sheep and rabbit dung were less pronounced and insignificant regarding the seedling emergence, but there was a clear contrast between the seed density assessed in the climate room experiment and the dung-borne seedlings in the field experiment. The emergence success in the field was much lower: without trampling only 5 or 7 % of the potential in the climate room,

but with trampling values were 3.6- or 2-fold higher. The trampling effect can be considered, to some degree, as similar to the crumbled dung which was used in the climate room. It is self-evident that optimised and controlled growing conditions in a climate room are beneficial for germination and establishment of plants while natural conditions are mostly harsh, as was also found in previous studies (Welch 1985; Auman et al. 1998; Mouissie 2004; Eichberg et al. 2007). Nevertheless, it was remarkable that *Helianthemum nummularium* ssp. *obscurum* exclusively emerged in the field on sheep dung but never in the climate room. The seed size often plays a crucial role concerning seed dispersal. Species which bigger seeds neither emerged in the climate room nor in the field. We assume that they do not survive digestion by herbivores, especially ruminants. The emergence success of graminoid competitors was very low. We found only one seedling of *Cynodon dactylon* in the climate room and *Poa angustifolia* emerged only once in the field.

The impact of trampling (question 3)

Plots with dung and particularly those with trampling treatment in addition harboured most plant species. This conspicuously indicates the importance of trampling as a facilitative post-dispersal process which had not previously been completely confirmed. Trampling on dung led to a significant increase in mean dung-borne seedlings and species numbers compared to dung plots without trampling treatment. A number of single species benefited from trampling, and no species was clearly adversely affected. The impact of trampling was particularly obvious in the case of sheep-dung pellets. Indeed, sheep-dung pellets without trampling treatment showed 3.6-fold lower numbers of seedlings than plots with pellets which were cracked by trampling. But also trampled rabbit-dung pellets had about twice the number of seedlings as the non-trampled ones. A positive effect of trampling on plant regeneration has been shown also for non-dung-embedded seeds lying on the ground (Wessels-de Wit & Schwabe 2010). Small-scale disturbances, especially those performed by digging rabbits, can create bare soil patches, which are crucial for seedling establishment in various grassland types (Jentsch et al. 2002; Bakker & Olff 2003). We found that trampling on dung, placed in bare soil patches, enhanced seedling establishment additionally, which emphasises on one hand the significance of gaps in dry grasslands and on the other hand the potential of post-dispersal processes like trampling.

The proportion of annual species emerging from dung was high but with trampling even higher. Some species exclusively emerged on plots with trampling treatment but never without trampling. However, trampling also facilitated the germination of species from sheep-dung plots. So, the emergence of ubiquitous species like *Chenopodium album/strictum*, *Oenothera biennis* s.l. or *Verbascum phlomoides* was due to trampling very high in sheep dung. The seedling emergence

with trampling treatment might even be stronger since we cannot exclude a potential underestimation of dung-borne seedlings on plots with trampling treatment, because some seeds may have been separated from the dung substrate during the trampling process. After trampling the dung formed a relatively compact layer on the soil and only seedlings from this layer were included in our records.

We infer that the most important impact of trampling is, particularly in the case of sheep dung, the cracking of the hard pellets' surface, and for both dung types the amplification of the dung's surface. Hence, dung-embedded seeds obtain a better light and water supply after trampling. Additionally, the dung layer may provide dung-borne seedlings with nutrients even before the roots of the seedlings enter the soil underneath for a further nutrient supply. For larger dung-embedded seeds a further positive effect of trampling may be an incorporation into the soil (Eichberg et al. 2005). A germination experiment conducted by Wessels-de Wit & Schwabe (2010) revealed that the relatively large seeds of *Cynoglossum officinale* almost exclusively germinated in a buried condition. Large seeds are assessed to require less light for germination than smaller ones (Baskin & Baskin 1998). However, on a community level this effect seems less important in our experiment, since these populations comprise mostly small-seeded species which depend on high ratios of light for a successful germination and establishment.

The fruiting success of dung-borne seedlings in the field experiment was high (21-31 %) and again, plants profited significantly by preceding trampling. Particularly annual and biennial species which had a high emergence success reached their fruiting stages within the 2-yr census period. Hence, trampling on one hand facilitated the emergence success and on the other hand even enhances the fruiting success. Eichberg et al. (2007) found only 0.4 % of sheep-dung-borne seedlings reaching fruit ripeness, which is in clear contrast to our findings. This is probably caused by differences in the treatments, study sites and study years. The study by Eichberg et al. (2007) was conducted with untrampled dung, in pioneer plant community stages and in the extremely dry year 2003. The sandy pioneer stages are known for their harsh environmental conditions for plant germination and establishment, whereas the conditions of our site are more consolidated and mesic.

Effects on target species (question 4)

TSR_{qual} of the seed pools contained in sheep and rabbit dung were reduced as compared to the index of the actual paddock vegetation. The TSR_{quant} was slightly but significantly higher for rabbit than sheep dung. These results are probably again caused by dietary preferences and differences between the two animal species. The preference of sheep for tall growing species, which are often ruderals (Artemisietea species), has been shown by Stroh et al. (2002).

Trampling, however, enhanced the relative emergence success of target species markedly, especially in the case of sheep dung. As a result, both TSR indices of both dung types are much enhanced by trampling and exceed those of the dung seed potential. This is due to the higher emergence of habitat-typical species (6 species in the field, 9 in the climate room) than that of non-target species (4 in the field, 17 in the climate room). Hence, the harsh environmental conditions are beneficial for the relative success of target species as a group (environmental filter).

The fruiting success of target species or individuals, however, was not significantly influenced by trampling and, in this development stage, the TSR indices are reduced again. This is in strong contrast to results of Eichberg et al. (2007): they found predominantly target species and even threatened target species emerging out of sheep dung, and the latter species group had very great fruiting success (80 %) whereas non-target species never set fruits.

In conclusion, sheep trampling in extensively managed sand grasslands with short grazing periods and long periods of plant re-growth has a significant positive impact on the post-dispersal development of many sheep-dispersed seeds. Sheep play a multifaceted role in dispersal processes: after endozoochoric transport they act as sort of “gardeners” not only for sheep-dispersed seeds, but also for those dispersed by rabbits.

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5. Chapter 5

General discussion

Knowledge about succession-driving factors and disturbance processes is a matter of great interest for threatened ecosystems in Central Europe. On one hand, increasing nitrogen depositions can cause an increase of competitive and ruderal plant species and also a decrease of site-specific plants in open sandy grasslands; on the other hand, these ecosystems are threatened due to changes in land use and the isolation of populations by fragmentation. This thesis was focused on the impact of nutrients in early-successional sand pioneer grassland, and the impact of disturbance regimes at different severities (sheep grazing, rabbit grazing, drought or fallow) in mid-successional grassland stages with regard to the successional development. In the last experiment I wanted to elucidate the post-dispersal fate of seeds that had been embedded in either sheep or rabbit dung, after a trampling and disturbance regime.

Succession

In general, succession can be influenced by biotic as well as abiotic factors like pH, (macro)climate, soil moisture and texture, the community's response to disturbance, species life histories, species interactions, plant establishment, competition and nutrient dynamics (Prach & Rehounková 2006; Prach et al. 2007; Walker & del Moral 2008). Concerning the last of these factors, especially the balance between N and P levels in both soils and plants can affect successional processes (Sterner & Elser 2002). Studies by Süss et al. (2004, 2010) in sand ecosystems of our area have demonstrated that the speed of succession is dependent on the vegetation type and nutrient availability. Permanent plots in early-successional stages of sand vegetation on nutrient-poor soils were relatively stable for over 13 years (Süss et al. 2010). In base-rich inland sand ecosystems the typical successional pathway leads from pioneer stages of Koelerio-Corynephoretea vegetation to species-rich stands of Allio-Stipetum vegetation (Süss et al. 2010).

The nutrient addition experiment in Chapter 2 gave evidence for two successional pathways in an early-successional community: one, which reflects the supposed "typical" line, and another one, which was clearly separated. But for most analysed parameters the separation into these two pathways was not detectable until a "lag phase" of about five years had elapsed. As shown within this chapter, nutrient addition led to an accelerated rate of succession because plots with N and P addition progressed approximately 1.5-fold further (see DCA diagram) during the years than the other plots. Nevertheless, the altered course of succession due to nutrient

enrichment was as expected and, for example, the accumulation of litter was enhanced or the cover of cryptogams decreased. Bryophytes diminished during succession as reported by Storm & Süss (2008) in initial sand ecosystems or in acidic dry grassland by Hasse & Daniëls (2006). Hence, the course of succession in our ecosystem type can be correlated with the development of non-typical species-poor vegetation stages especially when habitats show increased P-values (Süss et al. 2004).

Chapter 2 has shown that early successional species like small or short-lived species but also species of other ecological strategy types were not promoted by nutrient application, or they were even more or less displaced or gradually replaced by mid- and late-successional species or by dominant and/or competitive graminoids. Species which increase during succession are often more competitive (Römermann et al. 2008). This is also consistent with the observation by Süss et al. (2010) that vegetation stands on nutrient-rich soils developed very rapidly into ruderalised vegetation, whereas the cover of competitive graminoids strongly increased within two years. In addition, neighbourhood effects like the local seed rain can affect the earlier phase of succession (Baasch et al. 2009). The seed rain in our study consisted in part of autochthonous seeds but, nevertheless, most were allochthonous seeds, and among them mainly non-target species like different trees or ruderal herbs.

In Chapter 3, the community's response to different disturbance regimes was analysed. Beside the decline of species numbers on plots with sheep and rabbit exclusion there was a significant increase of litter cover shortly after the ungrazed plots were created due to fencing. The litter consisted mainly of competitive graminoids. Kahmen et al. (2002) assessed a negative change in species composition on fallow sites due to litter accumulation, an advanced succession or the establishment of woody species. The DCA has shown that the trajectories on the plots with intensive rabbit grazing and the plots with sheep and rabbit grazing were very similar, which is an indication for overgrazing due to rabbits. Furthermore, it was shown that the slightly ruderalised plots were less stable than the typical ones, if severe biotic disturbance occurred in our system. Nevertheless, the number of species slightly increased after the decline of rabbit population densities.

In addition, the experiments in Chapters 2 and 3 demonstrated the severe impact of drought, which occurred in the extraordinary year 2003. There was a pronounced decline of predominantly annual species in early- as well as mid-successional stages of sandy grassland at the study site. However, most species completely recovered in the following year.

The long-term study in Chapter 3 has on one hand clearly demonstrated the great potential for recovery and therefore resilience of our ecosystem, and on the other hand the benefit of extensive sheep grazing as conservation and succession-retarding measurement.

Nutrients

Inappropriate additions of fertilisers are known to be the cause for new shifts in trajectories (Walker & del Moral 2008). Additionally, an enhanced airborne nitrogen deposition can lead to an increase in vegetation density, threaten endangered species or decrease plant diversity (e.g., Gough et al. 2000; van der Hoek et al. 2004; Lanta et al. 2009). The impact of different types of nutrient addition on early-successional stages of threatened sandy grassland was analysed in Chapter 2. The use of the previous experiment by Storm & Süss (2008) for further investigations has shown that there was neither an influence on phytodiversity nor on community structure within the first four years of treatment, but afterwards, two successional pathways could be distinguished, a typical one on plots without N in high dosage, and a slightly accelerated one on plots with high dosage N and P. Huberty et al. (1998) pointed out, that the community response to N addition primarily is expressed through changes in community structure.

Furthermore, it could be experimentally shown in Chapter 2 that the species number and the cover of threatened species ("Red Data" species) diminished after five years of nutrient addition. Many of them were target species and belong to early-successional stages of the analysed community. In contrast, above-ground phytomass production of phanerogams was more than 2-fold higher by the N, NP, NPK and NPKM treatments, which is in line with Willems et al. (1993) or Gough et al. (2000). Also the cover of tall plants, "csr"-strategy types or competitive graminoids increased with N and P addition. An expected grass encroachment for mid-successional grassland stages in our area was already pointed out by Süss et al. (2004). Most individual species were facilitated by N and P additions; they grew taller or had more fruits and/or seeds, whereas legumes profited by N addition only in combination with macro- and micronutrients. This indicates the co-limitation of the main element N by P, which is in line with different authors (e.g. Bobbink 1991; Morecroft et al. 1994; Kooijman et al. 1998; Janssens et al. 1998; Mamolos et al. 2005; Storm & Süss 2008).

It was concluded by Stevens et al. (2004) that long-term chronic N depositions have significantly reduced plant species richness and that especially species adapted to infertile conditions are systematically reduced by high N depositions. In contrast, the experiment in Chapter 2 revealed that there were no or only minor effects of a moderately increased atmospheric nitrogen deposition for a few parameters in single years, which probably can be neglected. For the analysed timeframe an increase in vegetation density, grass dominance or a loss of species diversity due to an enhanced airborne nitrogen deposition can be excluded, which is consistent with Wilson et al. (1995).

The addition of a carbon source was often discussed as a useful tool for restoring N-limited plant communities and, hence, as restoration measure (e.g., Török et al. 2000; Blumenthal et al. 2003). Furthermore, an experiment by Alpert & Maron

(2000) could show that carbon addition can help counteract the invasion of grasslands by non-native plants, predominantly grasses, if the invasion is N-promoted. Other authors, however, found no significant effects on the vegetation by adding carbon (Morecroft et al. 1994; Corbin & D'Antonio 2004). The DCA diagram in Chapter 2 has revealed a slightly separated position of plots with C addition after several years, indicating a course of succession which is typical and contrary to the N+ treatment plots. Accordingly, the addition of carbon seems to be a beneficial measure but effects may be visible only after a longer period of treatment.

This experiment gave evidence for some negative aspects like changed successional lines, an increase of graminoids or the decrease of phytodiversity in a pioneer grassland due to enhanced nutrient inputs. It could be demonstrated that long-term experiments are necessary to investigate all aspects of nutrient addition.

Grazing

Extensive sheep grazing in low-productivity ecosystems can be an effective management method regarding the goals of nature conservation. Recently, this was highlighted by several studies for our model system (Stroh et al. 2002; Schwabe & Kratochwil 2004; Schwabe et al. 2004). Chapter 3 was focused on the influence of different grazing severities (extensive sheep grazing, intensive rabbit grazing, without grazing) and their impact on the studied site.

Sheep grazing has reduced tall-growing plant species and primarily sheep-grazed plots have shown a lower litter cover and a higher percentage of bare ground, as also found by several authors (Eldridge & Myers 2001; Croft et al. 2002; Hellström et al. 2003). Grazing and trampling by sheep in moderate intensities are positive related disturbance effects, which can maintain the structure of the study site. Sheep grazing as a conservation management tool can lead to variations in species and trait composition compared to other management methods like burning or fallow, which was observed in calcareous grasslands in south Germany (Kahmen et al. 2002).

The positive impact of sheep grazing may apply only if there are no further, stronger and counteracting disturbance effects like high rabbit densities in the community. This is depicted by the ordination diagram within Chapter 3: plots under moderate sheep grazing intensities were very close together between the first years of the study, and species numbers were quite high. Afterwards, the impact of sheep grazing appeared to be overlaid by the rabbits' influence due to the strong increase of the rabbit population, which caused the strong decline in species numbers. The development of the plots with rabbits and the plots with combined sheep and rabbit grazing was very similar. Furthermore, the high phytomass extraction rates have shown that rabbits very selectively extracted the Plant Functional Types "legumes" and "other forbs" compared to "graminoids". It is assumed that rabbits are able to compensate times of low phytomass production levels by grazing in fields near the studied site (Faust et al. 2007). In addition, there was a very destructive impact of

rabbits on inflorescences (including the prevention of flowering of many plant individuals), as was already described by Farrow (1917), Watt (1962) or Kiffe (1989).

In contrast, a lack of disturbance has favoured spontaneous succession on plots without grazing and has shown results quantitatively similar to those of intensive rabbit grazing or overgrazing. Ungrazed plots, for example after abandonment, show lower species numbers (Kahmen et al. 2002; Kahmen & Poschlod 2004) and often an encroachment of competitive graminoid species (Süss et al. 2004; Süss & Schwabe 2007; Süss et al. 2010). The results in Chapter 3 have clearly demonstrated that extensive grazing by sheep is necessary and maintains phytodiversity and community structure at our site if no more severe disturbances occur.

Post-dispersal processes and disturbance

Seed dispersal by epi- or endozoochory – in our landscape mainly by sheep – and the post-dispersal fate of dung-embedded seeds can be crucial for plant species especially in fragmented landscapes of threatened sandy grasslands (Eichberg et al 2007; Wessels-de Wit & Schwabe 2010). Furthermore, trampling is a common disturbance impact on livestock pastures (Hobbs 2006), but previous studies on trampling effects mainly focused on the gap-creating effect of hooves (Stammel & Kiehl 2004) or the increased seedling establishment in hoofprints (Harper 1977; Hach et al. 2005). It seemed likely that trampling also affects the germination and establishment of dung-embedded seeds, which was experimentally analysed in Chapter 4. In this experiment, plots with dung and sheep trampling treatment in addition harboured most plant species. Especially sheep-dung pellets showed a 3.6-fold enhancement of the number of seedlings with trampling, but also trampled rabbit-dung pellets had about twice as many seedlings as the non-trampled ones. Some species exclusively emerged on plots with trampling treatment but never without trampling.

It is inferred that the most important impact of trampling is the cracking of the hard pellets' surface, particularly in the case of sheep dung, and for both dung types the amplification of the dung's surface. Dung-embedded seeds obtain a better light and water supply after cracking by trampling. Trampling even facilitated the fruiting success of predominantly small-seeded annual and biennial species and the establishment success of target species. Thus, the harsh environment of the study site seems to be beneficial for site-specific plants. A further positive effect of trampling for (larger) dung-embedded seeds can be the incorporation into the soil surface, which was pointed out by Rotundo & Aguiar (2004) and Eichberg et al. (2005).

The experiment presented in Chapter 4 shows for the first time the importance of disturbance by trampling for dung-embedded seeds as a crucial post-dispersal process leading to successful establishment of plant individuals. Accordingly, the establishment success of plants after endozoochoric transport may be relevant for

sites with seed limitation due to fragmentation and therefore a spatial isolation. It can negatively affect the typical successional pathways, especially in early-successional vegetation stands, but only if the ratio of generalistic or competitive species in dung is high and habitats show nutrient enrichment.

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Summary

This thesis is focused on inland sand ecosystems, which are among the most threatened grassland types in Central Europe. These landscapes are highly fragmented and are inhabited by many endangered species in spatially isolated habitats. Recently, populations of the rare site-specific plant species decreased, the vegetation density increased and the typically open habitats became more and more ruderalised. As a reason, an enhanced nitrogen deposition and the abandonment of former extensively used grassland were discussed. Consequently, spontaneous succession can appear. To maintain community structure and population dynamics, different nature conservation management methods were introduced; in particular extensive sheep-grazing regimes became a suitable management tool in dry open habitats.

The aim of this thesis was to elucidate the impact of crucial abiotic and biotic factors on succession in threatened inland sand ecosystems in a successional gradient.

The main study site was the “Ehemaliger August-Euler-Flugplatz von Darmstadt“, a nature protection area in the northern Upper Rhine Valley of Germany. The characteristic plant communities of this site are considered highly threatened types in Central Europe according to the EU Habitats directive. The vegetation complex consists in the eastern part of early-successional stages of a pioneer Koelerion glaucae community, while in the western part mid-successional stages of Armerio-Festucetum trachyphyllae vegetation can be found. The substrates are primarily calcareous sands (Koelerion glaucae) with slight acidification of the topsoil (Armerio-Festucetum). The pre-grazing state in this system was characterised by a mowing regime during the military use and afterwards only by very extensive mowing and mulching. Sheep grazing was established in the area in the years 1999/2000.

Nutrient increase, e.g. by atmospheric nitrogen deposition or transfer of soil particles, is a major threat for many types of endangered open vegetation. As a model system we used threatened sandy grassland, where a nutrient addition experiment in a five-fold replicated randomised block design was started in the year 2000. We analysed the whole data set for a nine-year period and ran extended approaches in the years 2007 to 2009. We added nitrogen in low dose (n) to simulate an enhanced atmospheric deposition, nitrogen in high dose (N), nitrogen in high dose in combination with different micro- or macronutrients (NP, NPK, NPKM), phosphorus (P), and a carbon source (C) to immobilise plant-available nitrogen to our experimental plots. Additionally, seed limitation was tested by assessing the local seed rain. The data set was analysed by means of detrended correspondence analysis (DCA) and linear mixed models.

The DCA revealed two successional pathways: one line typical for threatened sandy grassland, and another one which was accelerated and clearly separated from the typical one. These separations were only detectable after a "lag phase" of about five years. As a general trend phytodiversity diminished on all plots, but the decrease was significantly stronger on plots with high-dose N, which have also shown higher turnover ratios. Site-specific species from pioneer stages (strategy type "stress-tolerators" and "ruderals") and "Red Data" species decreased with nutrient addition. Additionally, we observed an increase in cover of tall plants, geo- and hemicryptophytes, "competitors/stress-tolerators/ruderals" and competitive grasses on plots with high-dose N. The above-ground phytomass production of phanerogams was up to 3-fold higher following N, NP, NPK or NPKM treatment, but it was significantly lower in the case of cryptogams. In contrast, low-dose nitrogen and phosphorus only had no impact on any species except legumes, which were facilitated predominantly by P. The extended approach has shown that most plants were responsive to nutrient addition and grew taller or set more fruits or seeds. In the local seed rain many autochthonous and allochthonous species were found. Anyhow, most abundant species were non-target species and even *Calamagrostis epigejos* caryopses were found.

It could be shown by a field experiment that floristic structure, successional lines, phytodiversity and plant strategies of the studied system changed after a five-year period and a threatened vegetation type was gradually replaced by one with dominant and/or competitive species. These findings emphasise the importance of long-term observations for the study of effects caused by nutrients.

I used a long-term field experiment lasting 10 years for further investigations concerning the effects of sheep grazing as a type of moderate disturbance. As "experiments by nature" happened during this time period, we were also able to study severe biotic (rabbit grazing) and abiotic (drought) disturbances, examining the recovery and resilience of the system after these severe disturbances.

Within a six-fold replicated randomised split-plot design, 25-m^2 plots of Armerio-Festucetum trachyphyllae vegetation were studied from 2000-2009 in the northern upper Rhine valley (Germany). We analysed sheep-grazed and non-grazed plots (both with very low rabbit impact until the first half of 2005). In 2005 we established an additional plot type without rabbit and sheep grazing. Severe rabbit impact was studied in detail from 2006 to 2008 concerning flower resources, seed production, endozoochorous seed dispersal and phytomass extraction. Data were analysed by ordination methods and mixed linear models.

Moderate disturbance by sheep grazing maintained species diversity in times of low rabbit densities. Severe drought in 2003 resulted in a marked decrease of species numbers, but the system recovered already in 2004. The subsequently analysed "high rabbit impact" resulted in decreases of species numbers, cover of bryophytes, flower quantities and seed content in faeces. Species numbers also declined on plots without

rabbit grazing, but for different reasons. Shifts in phenological phases due to rabbit grazing were not observed, but the sum of flowers and number of flowering species decreased. After the decline of the rabbit population, species numbers slightly increased in 2009. Non-grazed plots showed an increase of litter.

Despite severe disturbances by rabbits or drought, the community structure was relatively stable, especially in the case of non-ruderalised plots, and showed only slight changes. We developed a conceptual model showing the high potential of recovery and resilience even in the case of severe disturbances.

Besides direct grazing effects like the creation of gaps by extensive livestock grazing, previous studies have shown benefits of seed dispersal (endo-, epizoochory), but little was known about post-dispersal processes such as trampling effects. We investigated the role of sheep trampling for the post-dispersal fate of dung-embedded seeds in sheep and rabbit dung and hypothesised a positive impact for the establishment of seedlings as a consequence of cracking the dung pellets. Sheep and rabbit dung was collected from threatened sandy grassland, and its seed potential was tested in a climate room. In a factorial field experiment we assessed the effects of trampling (using sheep-hoof replicas) and dung type on seedling emergence and fruiting success.

For both dung types seedling emergence in the field was only 5 or 7 % of the potential without trampling but 18 or 14 % with trampling. Plots with trampled sheep or rabbit dung both showed significantly more seedlings (3.6- or 2.1-fold), more species (2.4- or 1.9-fold) and more fruiting seedlings (3.9- or 2.6-fold) and fruiting species (2.1- or 1.9-fold) compared to non-trampled dung plots. However, not only target species profited from trampling, but also non-target species. This is disadvantageous regarding nature conservation aims, but the proportion of target species was clearly increased by trampling.

Sheep play a multifaceted role in dispersal processes: after endozoochoric transport they act as a sort of “gardener” not only for sheep-dispersed seeds, but also for those dispersed by rabbits.

Zusammenfassung

Die vorliegende Arbeit konzentriert sich auf Sandökosystemen des Binnenlandes, die zu den gefährdetsten Offenland-Lebensräumen Zentraleuropas gehören. Diese Landschaften sind in hohem Maße fragmentiert und beherbergen viele bedrohte Pflanzenarten in räumlich isolierten Habitaten. In letzter Zeit wurden ein Rückgang von Populationen mit seltenen gebietsspezifischen Arten, eine Erhöhung der Vegetationsdichte und die Ruderalisierung von typischen Offenhabitaten beobachtet. Begründet wurde dies mit erhöhten Stickstoffdepositionen und mit der Aufgabe von ehemals extensiv genutztem Ackergrünland. Als Folge kann spontane Sukzession auftreten. Zum Erhalt von Gemeinschaftsstrukturen und Populationsdynamiken wurde der Einsatz verschiedener Naturschutz-Pflegemaßnahmen erforderlich. Aus diesem Grund haben sich in trockenen Offenhabitaten insbesondere extensive Schaf-Beweidungsregimes zu einer geeigneten Pflegemaßnahme entwickelt.

Das Ziel dieser Dissertation lag in der Aufklärung von zentralen abiotischen und biotischen Einflüssen auf Sukzessionsprozesse in bedrohten Sandökosystemen des Binnenlandes entlang eines Sukzessionsgradienten.

Als Hauptuntersuchungsfläche diente das Naturschutzgebiet „Ehemaliger August-Euler-Flugplatz von Darmstadt“ in der nördlichen Oberrheinebene in Deutschland. Die charakteristischen Pflanzengesellschaften dieses Gebiets gehören zu den hochgefährdetsten in Zentraleuropa entsprechend den EU-Richtlinien für Biotope. Der Vegetationskomplex besteht im östlichen Teil aus frühen Sukzessionsstadien einer Koelerion glaucae-Pioniergesellschaft, der westliche Teil aus mittleren Sukzessionsstadien des Armerio-Festucetum trachyphyllae. Das Bodensubstrat besteht primär aus kalkreichem Sand (Koelerion glaucae) mit einer leichten Versauerung im Oberboden (Armerio-Festucetum). Vor der Einführung von Beweidung waren die Flächen während der militärischen Nutzung durch ein Mahdregime gekennzeichnet, danach erfolgte nur noch extensive Mahd und Mulchen. Schafbeweidung wurde im Gebiet in Jahren 1999/2000 etabliert.

Nährstoffzufuhr, durch z. B. atmosphärische Stickstoffdeposition oder der Transfer von Bodenpartikeln, ist eine große Bedrohung für viele gefährdete Offenland-Vegetationstypen. Als Modellsystem dienten bedrohte Sandrasen, auf denen im Jahr 2000 ein fünffach-repliziertes Nährstoffapplikationsexperiment in randomisiertem Blockdesign gestartet wurde. Der gesamte Datensatz wurde für neun Jahre untersucht, wobei im Rahmen dieser Arbeit in den Jahren 2007 bis 2009 zusätzliche Spezialuntersuchungen durchgeführt wurden. Auf die Experimentalflächen wurden folgende Nährstoffe appliziert: Stickstoff in schwacher Dosis (n) zur Simulation atmosphärischer Deposition, Stickstoff in hoher Dosis (N), hochdosierter Stickstoff in Kombination mit verschiedenen Mikro- und Makronährstoffen bzw. -elementen (NP, NPK, NPKM), Phosphor (P) und eine Kohlenstoffquelle (C) zur Immobilisierung des

pflanzenverfügbaren Stickstoffs. Zudem konnte die Samenlimitierung mittels des lokalen Samenregens gemessen werden. Der Datensatz wurde mithilfe einer „Detrended Correspondence Analysis“ (DCA) und gemischt-linearen Modellen ausgewertet.

Die DCA zeigte zwei Sukzessionspfade auf: einen, der typisch für bedrohte Sandrasen ist, und einen, der eine beschleunigte Sukzession dokumentiert und sich zudem klar vom typischen Pfad abgrenzt. Diese Auftrennung war erst nach einer „Lag Phase“ von ungefähr fünf Jahren deutlich. Als allgemeiner Sukzessionstrend verringerte sich die Phytodiversität auf allen Flächen, jedoch war die Abnahme auf Flächen mit hochdosiertem Stickstoff signifikant höher, welches sich auch durch erhöhte Turnover-Raten auf diesen Flächen zeigte. Habitat-spezifische Arten der Pionierstadien („Stress-Strategen“ oder „Ruderal-Strategen“) und „Rote Liste“-Arten nahmen durch Nährstoffapplikation ab. Zugleich nahm aber die Deckung von hochwüchsigen Pflanzen, Geo- und Hemikryptophyten, „Konkurrenz-Stress-Ruderal-Strategen“ und kompetitiven Gräsern auf Flächen mit hochdosiertem Stickstoff zu. Die oberirdische Phytomasseproduktion der Phanerogamen verdreifachte sich durch N, NP, NPK oder NPKM-Applikation, sie war jedoch signifikant niedriger im Falle der Kryptogamen. Im Gegenzug zeigte die Behandlung mit niedrigdosiertem Stickstoff und Phosphor keinen Einfluss mit Ausnahme der Leguminosen, die insbesondere von P profitierten. Die Spezialuntersuchungen zeigten, dass fast alle untersuchten Arten auf die Nährstoffapplikation reagierten und höher wuchsen oder mehr Früchte bzw. Samen produzierten. Der lokale Samenregen bestand sowohl aus vielen autochthonen als auch allochthonen Arten. Die Arten mit der höchsten Abundanz waren dennoch keine Zielarten, und sogar Karyopsen von *Calamagrostis epigejos* konnten nachgewiesen werden.

Das Freilandexperiment konnte zeigen, dass sich die floristische Struktur, die Sukzessionslinien, die Phytodiversität und die Pflanzenstrategien des untersuchten Systems nach einer fünfjährigen Phase änderten und ein gefährdeter Vegetationstyp teilweise durch einen mit dominanten und/oder kompetitiven Arten ersetzt wurde. Diese Ergebnisse zeigen die Bedeutung von Langzeitbeobachtungen für die Untersuchung von nährstoffinduzierten Effekten.

Im Rahmen eines zehnjährigen Langzeitexperiments im Freiland habe ich weitere Untersuchungen in Bezug auf Schafbeweidung als ein Beispiel für Störung mittlerer Intensität durchgeführt. Während dieses Zeitraums traten „Experimente der Natur“ auf, die in Form von schweren biotischen (Kaninchenbeweidung) und abiotischen (Trockenheit) Störungen untersucht wurden, um die Faktoren „Erholung“ und „Resilienz“ zu überprüfen.

In den Jahren 2000 bis 2009 wurden innerhalb eines sechsfach replizierten und randomisierten Split-Plot-Designs 25 m^2-Flächen von Armerio-Festucetum trachyphyllae-Vegetation in der nördlichen Oberrheinebene (Deutschland) untersucht. Wir analysierten Schaf-beweidete und unbeweidete Flächen (beide mit

einem nur sehr geringen Kaninchencheneinfluss bis zur ersten Hälfte des Jahres 2005). Im Jahre 2005 wurde ein zusätzlicher Flächentyp mit Ausschluss von Kaninchen- und Schafbeweidung etabliert. Der starke Kaninchencheneinfluss wurde ausführlicher in den Jahren 2006 bis 2008 hinsichtlich Blütenressourcen, Samenproduktion, endozoochorer Samenausbreitung und Phytomasseentzug untersucht. Die Daten wurden mithilfe von Ordinationsverfahren und gemischt-linearen Modellen ausgewertet.

Mittlere Störung durch Schafbeweidung konnte in Zeiten eines niedrigen Kaninchenbesatzes die Artendiversität aufrecht erhalten. Durch die starke Trockenheit im Jahre 2003 nahmen die Artenzahlen deutlich ab, das System hatte sich aber bereits in 2004 wieder erholt. Der danach aufgetretene hohe Kaninchencheneinfluss verursachte eine Abnahme der Artenzahlen, der Moosdeckung, der Blütenmengen und des Samengehalts im Dung. Die Artenzahlen nahmen auch auf den Flächen ohne Kaninchenbeweidung ab, dies hatte jedoch andere Ursachen. Es konnten keine Verschiebungen der phänologischen Phasen bedingt durch Kaninchenbeweidung beobachtet werden, aber die Blütensummen und die Anzahl blühender Arten nahmen signifikant ab. Nach dem Rückgang der Kaninchenpopulation zeigten die Artenzahlen einen leichten Anstieg in 2009. Unbeweidete Flächen zeigten einen Anstieg von Streu.

Trotz der starken Störungen durch Kaninchen oder Trockenheit war die Gemeinschaftsstruktur relativ stabil, welches insbesondere auf die nicht-ruderalisierten Flächen zutraf, die sich nur wenig veränderten. Wir konnten ein konzeptionelles Modell entwickeln, dass das hohe Erholungs- und Resilienzpotential im Falle starker Störungen aufzeigt.

Abgesehen von direkten Beweidungseffekten wie die Schaffung von Lücken durch extensive Viehbeweidung konnten vorangegangene Studien den Nutzen durch Samenausbreitung (Endo-, Epizoochorie) zeigen, aber dennoch ist wenig über Prozesse nach der Ausbreitung bekannt wie beispielsweise Effekte durch Trampeln. Ich untersuchte die Rolle der Hufeinwirkung („trampling“) von Schafen auf das Schicksal von Samen, die in Schaf- und Kaninchendung eingeschlossenen waren, nach deren Ausbreitung und stellte die Hypothese auf, dass die Etablierung von Keimlingen begünstigt wird als Folge des Aufbrechens der Dungpellets. Schaf- und Kaninchendung wurde in gefährdeten Sandrasen gesammelt und deren Samenpotential in einer Klimakammer getestet. In einem faktoriellen Freilandexperiment wurden die Effekte des Trampelns (mittels Schafhuf-Replikaten) und des Dungtyps auf das Keimlingsaufkommen und den Fruchterfolg festgestellt.

Das Keimlingsaufkommen im Freiland entsprach für beide Dungtypen nur 5 bzw. 7 % des Potentials ohne Trampeln, mit Trampeln jedoch 18 bzw. 14 %. Flächen mit betrampeltem Schaf- oder Kaninchendung zeigten signifikant mehr Keimlinge (3,6- oder 2,1-fach), mehr Arten (2,4- oder 1,9-fach) und mehr fruchtende Individuen (3,9- oder 2,6-fach) und fruchtende Arten (2,1- oder 1,9-fach) verglichen mit den

Flächen ohne betrampeltem Dung. Es profitierten nicht nur Zielarten durch das Trampeln, auch Nicht-Zielarten. Dies könnte sich nachteilig hinsichtlich der Naturschutzziele auswirken, aber der Anteil an Zielarten war dennoch deutlich erhöht durch das Trampeln.

Schafe spielen eine facettenreiche Rolle in Ausbreitungsprozessen: nach dem endozoochoren Transport haben sie eine Art „Gärtnerfunktion“ nicht nur für Schaf-ausgebreitete Samen sondern auch für die Samen, die durch Kaninchen ausgebreitet werden.

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Lebenslauf

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Eidesstattliche Erklärung

Ich erkläre hiermit an Eides statt, dass ich die vorliegende Dissertation selbständig und nur mit den angegebenen Hilfsmitteln angefertigt habe. Ich habe noch keinen Promotionsversuch unternommen.

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